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THE SYSTEM OF PIT ORGAN LINES IN GYMNARCHUS NILOTICUS

BY

TORSTEN PEHRSON

(With 3 figures in the text)

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The sensory line canal system in Gymnarchus is in various respects different to that encountered in other Teleosts, and in Ganoids, as has been pointed out by ALLIS (1904). The usual canals exist, and follow the pattern typical in Teleosts. There is, thus, a long supraorbital canal connected posteriorly with the infraorbital canal. The mandibular canal is continued by the preopercular canal, which joins the main canal in the intertemporal region, and still more caudad there is on each side a short extrascapular canal, representing the vestigial supratemporal commissure canal. The innervation of the neuromasts is, also according to ALLIS, what is typical in Teleostomian fishes.

Yet there are several features characteristic of the canal system in this fish. One is that the canal system possesses very few pores, only one in the supraorbital canal, one in the infraorbital, one in the mandibular, one in the preopercular (in ALLIS's figure two are indicated but in all the specimens I have had the opportunity of examining there has never been more than one), one in the extrascapular and one in the supracleithral portion of the main body canal, thus 6 pores in all on each side of the head; also, the pores have the shape of narrow elongated tubes, which according to ALLIS do not open distally. In my specimens the long caudally directed tubes (fig. 3 p), which correspond to the pores, always have a minute opening in the skin, but in adult specimens it is not possible to discover any communication with the surface. The canals form thus an entirely closed system, at least in the adult. Even in young specimens that is practically the case as the openings of the tubes are so exceptionally small.

Furthermore, the temporal portion in the adult is enlarged and forms a wide flattened chamber over the labyrinth. Allis suggests that the whole canal

system has changed its function, and acts as a sort of accessory hearing apparatus.

I have had the opportunity of examining a number of young stages of Gymnarchus, originally with the purpose of following the development of the sensory line canal bones. The material at my disposal included two series of specimens, one from the earliest stages up to a body length of 17 mm, and one beginning with 32 mm body length and ending with a length of about 60 mm.

As the gap in the material unfortunately excluded from investigation the stages where the greater part of the canal bones take their origin, this part of the work had, so far, to be left to the future.

During the examination of the last mentioned older set of stages, my attention was attracted by a system of well developed lines of pit organs. That this system has escaped the eye of an investigator as keen as ALLIS is probably due to the fact that in adult specimens it is hardly possible to discern macroscopically. The skin of Gymnarchus is unusually thick and lacks scales, but on the other hand it is supplied with densely lying glandular organs, innervated from the trigeminus nerve. Already in the youngest of the adult specimens at my disposal, measuring 220 mm in body length, it is hardly possible, except in some few places, to distinguish any lines of pit organs.

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These lines have been studied in situ macroscopically in the heads of specimens of 32—58 mm length, and also in series of slides of specimens measuring 32, 41, 51 and 58 mm. From the 32 and 41 mm specimens reconstructions have been made. It has been possible to estimate the number of sense organs in the respective lines as well as to follow their innervation.

The relative size and shape of pit organs and glandular organs is clear from fig. 1. The glandular organs are irregularly scattered in the skin, but are more frequent on the anterior portion of the head. At the stages between 50 and 60 mm they grow considerably in size and in these stages the pit organs which have been lying quite superficially begin to sink into shallow pits.

In Teleosts the general pattern of the lines of pits in the head is on the whole congruent with the scheme described by ALLIS (1889) in Amia, the main difference being that the rostral comissure canal in Amia, and other Ganoids, is substituted in Teleosts by a line of pit organs. Also one, or several of the lines in Amia may be missing (ALLIS 1904, PEHRSON 1944 a). Other differences concerning the distribution of pit lines in Teleosts is the substitution of portions of sensory line canals with pit lines, and the differentiation from a sensory line canal of a line of superficial sense organs, which form a sort of secondary pit organ lines (PEHRSON 1944 a). Particulars about these questions will be dealt with further on in this paper.

Most of the pit organ lines which belong to the general scheme, mentioned above, are found in Gymnarchus. On the top of the head there is, thus, a

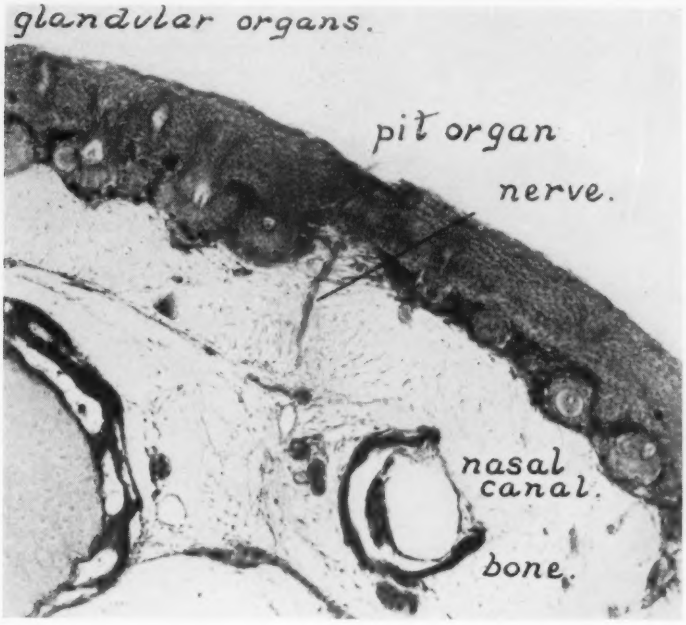

Fig. 1. Cross section through the nose of 58 mm. Gymnarchus showing a nasal pit organ, glandular organs and nasal latero-sensory canal with nasal bone and neuromast.

pattern of 6 lines (figs 2 a, b and 3). They are the well known 3 pairs of anterior, middle and posterior head lines. The homology of these lines is proved not only by their position, but also by their innervation, as they receive their nerves from the ramus ophtalmicus superficialis, from nervus glossopharyngeus, and from lateralis vagi, respectively. As a rule all three lines do not occur in Teleosts. In Esox only the middle line is represented, in the Siluroid Menidia (HERRICK 1899) there is also one, probably the posterior and in Salmo all three, although very short.

The length of the lines is also unusual; this applies chiefly to the anterior, and the middle line. The anterior lines are bent inward at a little more than a right angle, the rounded point being directed laterad. The middle lines run in a latero-caudal direction in a slight curve, and the short posterior lines run almost parallel with the medial portion of the middle lines. In the anterior line there are in a 41 mm specimen 13 sense organs on each side, in the middle 12. and in the posterior, which are situated in the medial prolongation of the extrascapular canals, only 7.

On the snout there are two lines. Most anteriorly lies one with chiefly caudal extension (fig. 2 b and 3 rpl). In the mid line it forms a short but sharp curve orad. The sense organs (in a 41 mm specimen 7 on each side) are innervated from branches of the ramus buccalis. This line is, thus, as

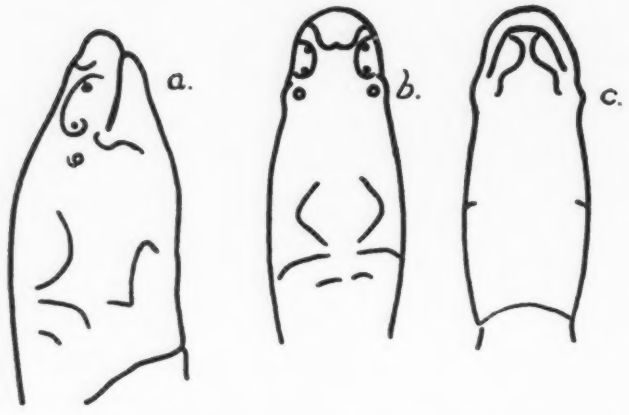

Fig. 2. Lateral *a*, dorsal *b* and ventral *c* views of head of 58 mm Gymnarchus showing pit organ lines.

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might be expected from its position, the rostral commissure, or supraethmoidal line of pit organs.

Posteriorly, and slightly laterally, is another line which runs in a curve above the two nasal openings (figs. 2 b and 3 npl). It begins laterally and orally to the anterior nasal opening, and ends caudally and ventrally to the posterior opening. In a 41 mm specimen it consists of not less than 21 sense organs on each side. They are all innervated from the ramus ophtalmicus superficialis by branches from the nerves supplying the supraorbital canal organs in the nasal portion. There is no line of pit organs described which corresponds to this one. The question of its homology has to be settled in a different way.

In Esox (PEHRSON 1944 a) there is a unique line of superficial sense organs, ventral to the antorbital portion of the infraorbital canal, and parallel with it. Its sense organs are innervated by ramus buccalis, which sends nerves to the neuromasts in the infraorbital canal as well. Now, it is proved that this infraorbital line of superficial sense organs, a line which in every respect resembles a normal line of pits, and has been erronously interpreted by ALLIS (1904) in Esox americanus, as a dislocated cheek line, arises in Esox during the ontogeny by means of a differentiation of the infraorbital latero-sensory line. This line like all the other latero-sensory lines in Esox arises as a superficial row of neuromasts, which increase in number during the development. Later during the ontogeny only a few neuromasts become enclosed in the future canal, while the majority of the sense organs are sorted out to form the above-mentioned superficial sensory line. Their origin is furthermore proved by the fact that they are supplied with nerves by the same branches as the organs enclosed in the canal (PEHRSON 1944 a).

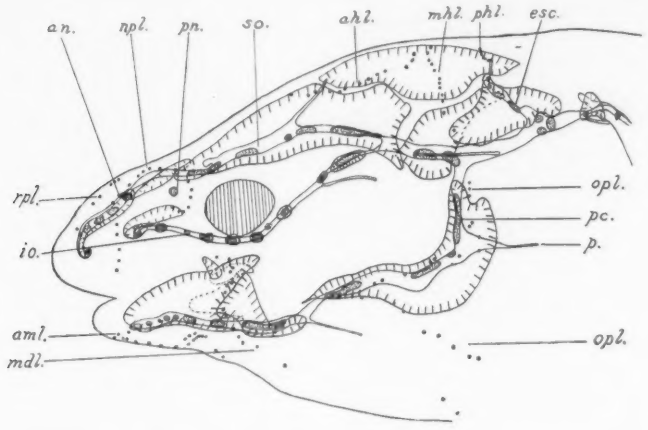

Fig. 3. Lateral view of head of 41 mm. Gymnarchus showing latero-sensory canal system with neuromasts and tube like pores, dermal bones and pit organs (small black dots). Reconstruction.

The relations between the "nasal" line of pit organs in Gymnarchus, and the nasal portion of the supraorbital canal, are the same as between the accessory antorbital line in Esox, and the antorbital canal line, both as far as the position is concerned and the innervation. The sense organs in the "nasal" line in Gymnarchus are innervated by the same branches as the neuromasts in the nasal latero-sensory canal. It seems probable that the same process which has been described in Esox has also occurred in Gymnarchus, only in the supraorbital line. The "nasal" line of pit organs in Gymnarchus is, thus, to be considered as a differentiation of the supraorbital canal.

Posterior to the mouth is another line of pit organs (figs. 2 a and 3 mdl). It is slightly S-like in shape, and crosses the mandibular line. It is homologous to the vertical mandibular line in Amia, which is evident both from the position, and from the innervation, by branches from the nervus mandibularis. It differs only from the normal conditions because of its unusual length. In the 41 mm specimen it consists of 15 sense organs.

Another line of pit organs innervated from the ramus mandibularis, is situated ventrally on the anterior end of the mandible on each side (figs. 2 c and 3 aml). Anteriorly it begins on each side of the mid line, and runs first almost straight mesiad. At the anterior end of the mandibular canal it makes a sharp bend, and then runs almost straight laterad. Like the "nasal" line described above, it does not correspond to any known line of pits, except possibly an anterior gular line. Yet it seems hardly possible to homologise it with such a line. Firstly, a gular line is, so far, not found in any Teleosts. Secondly, an anterior gular line should be a transversal line, whereas, here are two distinct lines, one on each side. Finally, these two lines are innervated

from the same branches of the mandibular nerve, as are the neuromasts in the mandibular canal. Thus it seems most probable that here is the same question of differentiation of a canal line as is described above concerning the "nasal" line. The same conditions are described from Esox (PEHRSON 1944 a) where a line of small sense organs in the anterior end of the mandibular canal line does not become enclosed in the canal, but multiplies and forms a seemingly independent line of pit organs. In Esox the development of this accessory pit line has been followed in detail, as was also the case respecting the antorbital line in Esox mentioned above. In Protopterus according to HOLMGREN (1942) there is a mandibular line of pit organs, which resembles the one mentioned above in Gymnarchus as to its course. From his illustration it seems to be a continuation of the primary mandibular line, and is called by HOLMGREN the primary oral line.

On the cheek of Amia are found two pit organ lines, the horizontal line situated more dorsally, and a vertical cheek line more ventrally. These two lines are described from Esox amongst the Teleosts (PEHRSON 1944 a). As pit organ lines seem to be abundantly developed in Gymnarchus even they might be expected in this fish. As a matter of fact there is a cheek line developed in Gymnarchus, yet it runs in a different way, and is more difficult to interpret. It begins a little ventrally to the place where the preopercular canal opens into the main canal, and runs first vertically ventrad, parallell with, and superficially to the preopercular canal. At the point where this canal bends perpendicularly orad it follows the bend of the canal, and runs for a short distance orad, still parallell with the canal. Then it turns in a sharp angle, and runs ventrad and caudad (figs. 2 a and 3 opl).

There are several possibilities as to the homologisation of this line. Near at hand is to suppose that it is a differentiation from the preopercular canal, thus a structure of the same kind as the "nasal", and the anterior mandibular line mentioned above. This idea is supported by the position of the line, as the vertical and the horizontal portions are practically congruent with the preopercular canal. Another possibility is that the line in question is the homologue of one, or both cheek lines of pit organs, the horizontal, and the vertical line, as two portions of the line run in those directions.

An examination of the innervation of the canal organs, and of the pit organs, gives the following result. The preopercular canal organs are supplied by two nerves, one from the horizontal part, and another from the vertical. In the 41 mm specimen they do not join to form a common truncus hyomandibularis until they have reached the ganglion. The nerves from the pit organs are not connected with either of these branches. This fact excludes the first alternative mentioned above, and it is obvious that the pit organ line cannot be derived from the canal. The nerves from the pit organs are connected with another branch, which joins the ganglion farther caudad than the truncus hyomandi-

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bularis. This nerve seems furthermore to receive threads which belong to the general cutaneous system, a circumstance, however, which will make more detailed investigation necessary, and falls outside the scope of the present paper. In any case, the place of the proximal junction of this branch seems, also, to exclude the second alternative. The line cannot be homologous to either of the two cheek lines of pit organs, as these lines are generally supplied by more distal branches of the truncus hyomandibularis.

Yet a third possibility remains. This theory is suggested by the conditions in Esox. In this fish (PEHRSON 1944 a) there is also an opercular system of pit organs. It is formed by some scattered organs situated on the dorsal part of the operculum, by a postero-ventral, comparatively short line, and of an anterior line. This last mentioned line is situated posterior to the preopercular canal, and begins on a level with the dorsal pore of this canal, runs first ventral in a vertical position, and then bends like the line in Gymnarchus, at a right angle on a level with the curve in the preopercular canal. The horizontal portion is comparatively short, and a centro-caudal continuation is lacking. Its sense organs are supplied by a special branch of the truncus hyomandibularis. Opercular pit organs have obviously escaped observation by earlier investigators, for in the literature they are only mentioned — except in Esox — by HERRICK (1899) in Menidia. There are in this fish, according to HERRICK, a row of four organs along the ventral edge of the operculum, and two or three more irregularly placed. They are supplied by the first branch of the ramus mandibularis, which, according to HERRICK's illustration, runs ventro-caudad.

It seems most probable that the line in question in Gymnarchus is an opercular line of pit organs, and nearest homologous to the anterior opercular line in Esox. Its shape does not contradict such a supposition, nor does the position, although the line has moved orad in Gymnarchus. As to the innervation it excludes practically any other explanation.

An interesting fact is that the ventral portion of this line corresponds, as far as the position is concerned, to the posterior gular line in Osteolepis.

The unusual frequency of surface sense organs in the head of Gymnarchus, refers with certainty to the conditions of the latero-sensory canal system, mentioned earlier in this paper. This system is not only located unusually deep in the skin, but is also entirely closed and has probably changed its functions. This has lead to the development, not only of the irregularly scattered surface glandular organs, which, as far as can be judged from their innervation are acting as some sort of sense organs, but also of surface organs of the pit organ type. Thus, the lines of pit organs, homologous to those in Amia, are better developed than is the case generally in Teleosts. Further new

lines have been formed by means of differentiation of the later-sensory canal system.

The mutual dependence of the various kinds of sense organs in fishes generally is apparent also from the conditions in, for instance Esox, Acipenser and Polyodon. In Esox (PEHRSON 1944 a) the neuromasts in the canals are comparatively few, whereas the pit line system in this fish is unusually well developed, and might — except for the length of the pit organ lines — be compared with that in Gymnarchus. In Acipenser on the other hand there is in the adult fish only one pit organ line existing, the middle head line with only one sense organ, and in Polyodon none (PEHRSON 1944 b). These two last mentioned fishes are, instead, equipped with an abundant number of so called nerv-sacs, surface organs interpreted as sense organs.

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REFERENCE LETTERS.

ahl, anterior head line of pits.
aml, anterior mandibular line of pits.
an, anterior nasal opening.
esc, extrascapular canal.
ic, infraorbital canal.
mdl, mandibular line of pits.
mhl, middle head line of pits.
n, neuromast.
npl, nasal line of pits.
opl, opercular line of pits.
p, canal pore.
pc, preopercular canal.
phl, posterior head line of pits.
pn, posterior nasal opening.
rpl, rostral line of pits.
so, supraorbital canal.

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CONTRIBUTIONS TO FOREBRAIN MORPHOLOGY IN DIPNOI

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I. INTRODUCTION.

In studying the text-books dealing with the comparative anatomy of the nervous system of vertebrates published during the last few decades, one is astonished at the scant notice given to the morphology of the dipnoan forebrain, and yet a cursory investigation shows that this section of the brain must have a certain significance in the comparative anatomy of the forebrain in lower vertebrates. It shows an interesting composition of primitive characters together with specific modifications characteristic of the different dipnoan species. KAPPERS does not mention the Dipnoi in the part of his "Vergleichende Anatomie des Nervensystems" (1920—21) dealing with the forebrain. In the second, enlarged American edition, published in 1936, KAPPERS and his American collaborators mention the dipnoan forebrain very cursorily in the chapter dealing with the forebrain of Ganoids and Teleosts. HALLER (1934) in the neurological section of "Handbuch der vergleichenden Anatomie der Wirbeltiere" mentions the dipnoan forebrain only twice in connection with the forebrain of the Amphibia; first when he points out that the latter "hat in seinem Bau viel Ähnlichkeit mit dem der Dipnoer", and again when remarking that the hemispere of Protopterus "besitzt keine Pars postforaminalis und erweist sich auch in dieser Hinsicht als primitiv" (p. 157).

Apart from the earliest works on Protopterus (OWEN 1839, SERRES 1863, FULLIQUET 1886) and Epiceratodus (HUXLEY 1876, BEAUREGARD 1881, WILDER 1887, SANDERS 1889), which contain mostly descriptions of the outer form

of the brain, there have been published some principal works on the forebrain of Dipnoi, which give rather a good idea of the general morphology of this brain part. The first to make a closer investigation of the dipnoan brain was BURCKHARDT (1892 b). He made a detailed study of the forebrain in Protopterus illustrated with excellent figures showing a large number of principal cyto-architectonical characters of this brain part. BURCKHARDT, however, interpreted some of the telencephalic cell areas erroneously, i. e. he placed the olfactory bulb in contact with the nasal sac. Further, he placed the corpus striatum in the dorsal part of the medial wall, and was of the opinion that the cortex of the tuberculum olfactorium constitutes a "lobus hippocampi". These errors have been pointed out by ELLIOT SMITH (1908) who, in his paper dealing with the structure of the telencephalon of Lepidosiren paradoxa, outlined the modern conception of forebrain morphology in dipneumonian lungfishes.

BING and BURCKHARDT's paper (1905) on the central nervous system of Epiceratodus corresponds to BURCKHARDT's work on Protopterus. But here also errors exist in some principal points. The authors are of the opinion that the "lingula interolfactoria", which is a very characteristic feature in the forebrain of Epiceratodus, constitutes an unparied epithelial membrane, forming the roof of a ventricle common to both hemispheres along almost their whole extension. HOLMGREN and VAN DER HORST (1925) in making an accurate cyto-architectonical and fibre-anatomical study of the brain of Epiceratodus, however, show that this "lingula" is an epithelial part of the medial hemispheric wall and therefore a paired structure. Consequently we have in Epiceratodus distinctly evaginated hemispheres and this evagination is not limited to the rostral parts of the telencephalon, which according to BING and BURCKHARDT should be the case.

The forebrain of the adult Protopterus has also been treated by HOLMGREN (1922), KUHLENBECK (1924) and GERLACH (1933). HOLMGREN, as result of the scantiness of his material, could not make any far-reaching investigation, but he pointed out that he found in Protopterus the same conditions as those found by ELLIOT SMITH in Lepidosiren. Further, he shows that the selachian and dipnoan forebrains have many structures which are built principally after a common plan. Nor was GERLACH's material sufficient for a more detailed investigation of cellular and fibre structures, and he makes scarcely any noteworthy contribution beyond the results of ELLIOT SMITH on Lepidosiren and HOLMGREN on Protopterus. The same applies to KUHLENBECK's investigation. The latter author has (1929 a) drawn a "Bauformel" of the forebrains of vertebrates. "Absicht dieser Arbeit ist also die Aufstellung streng morphologischen Bauformeln, welche, von den systematisch am tiefsten stehenden Formen ausgehend, stufenweise auseinander entwickelt werden können. Im Gegensatz zu den bisherigen Arbeiten über die Homologien der Endhirngebiete müssen daher

von vornherein unpräjudizierende und neutrale Bezeichnungen angewendet werden, welche lediglich auf die Bedeutung dieser Gebiete als Grundbestandteile des Bauplans Bezug nehmen." In working out these "Bauformeln", however, KUHLENBECK has considered the conditions in adult brains only. HOLMGREN (1922), for instance, has shown that pallial cortices exist in the embryonic stages of Selachians, which is not evident from KUHLENBECK's selachian "Bauformel". Such a "Bauformel", which does not take into consideration the ontogenetic development, cannot completely reflect the characteristic features in the structure of the telencephalon in different vertebrate groups, and gives rise easily to erroneous interpretations. This is also very much in evidence in SÖDERBERG's investigation (1922) of the ontogenetic development of the forebrain in Anura and Urodela. She has shown that the telencephalon in these animals does not constitute such a primitive type as had hitherto been supposed. On the contrary, we have traces here of more differentiated stages of development, a fact which is evident from the conditions in the embryonic amphibian telencephalon. HOLMGREN's and SÖDERBERG's investigations thus show the importance of ontogenetic development in the interpretation of the morphology and the phylogenetic position of the adult brain. There has been a tendency among neurologists to neglect this factor.

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Two papers exist on the ontogenetic development of telencephalon in Dipnoi. KERR (1902) describes this development in Lepidosiren, and GREIL (1913) has treated the corresponding conditions in Epiceratodus. Both these investigators show the principal features in the external form during different phases of the ontogenetic development. The way in which the telencephalic nuclei has been developed is not evident, however, from the papers in question. It is important to know this development in order to interpret those seemingly widely separated types of forebrains which exist in adult Dipneumonia and Monopneumonia. BING and BURCKHARDT have also cursorily treated the ontogenetic development of the brain of Epiceratodus in their paper mentioned above. The authors give some illustrations showing certain details in the cytoarchitectonical structures in the telencephalon of older embryonic stages, i. e. the distinctly developed pallial cortex. The authors, however, only note that "Dafür, dass in Stadium 48 im Gebiete des Vorderhirnes bedeutende Umgestaltungen vor sich gehen, sprechen die auf Textfig. 14—15 sichtbaren merkwürdigen Kerngruppierung, die wohl als Richtungslinie von Zellwanderungen aufzufassen sein dürften."

As I have at my disposal an abundant collection of embryonic stages of Protopterus annectens, I have tried in this paper to make a renewed investigation of the ontogenetic development of the dipnoan forebrain, especially with regard to the development of the different telencephalic cell areas, in order to explain some of the structures in the adult animals. Further, I want to verify whether forebrain ontogeny in Dipnoi, as compared with the corres-

ponding development in Amphibians, has any bearing upon the problem of the phylogenetic development of the brain of these two groups. HOLMGREN and VAN DER HORST have studied the fibre anatomy of the telencephalon in Epiceratodus, but as we have no data concerning the same structures in Protopterus, I have tried to make such an investigation with the material at my disposal.

In his paper on the development of the diencephalon in lower vertebrates, BERGQUIST (1932) expresses the opinion that in early ontogenetic stages there exist in this brain part certain areas which are distinguished by a more marked cell proliferation. These zones of proliferation ("Grundgebiete") which, according to BERGQUIST, give rise to homologue nuclei in different groups of lower vertebrates, are grouped around certain sulci ("Proliferationsfurchen"). I have investigated early stages of the telencephalon in order to determine what corresponds to BERGQUIST's "Proliferationsfurchen" and "Grundgebiete" in the diencephalon.

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This investigation has been performed at the Zootomical institute of the University of Stockholm, and I wish to express my sincere gratitude to the director of this institute, professor NILS HOLMGREN. I am indebted to him for advice and suggestions given to me during the course of the work, and for the plentiful collections of neurological material belonging to the institute, which he kindly placed at my disposal. Further, I am very much indebted to Dr. G. SVENSSON, the resourceful leader of the Swedish Gambia Expedition in 1931. Thanks to him the expedition was able to make very valuable collections, especially of lungfish material.

I should also like to express my sincere gratitude to the directors of the STIFTELSEN LARS HIERTAS MINNE, and the GUSTAF and ANNA RETZIUS FOUNDATION FOR SCIENTIFIC RESEARCH, from whom I have received grants towards my research work. I am also very much indebted to the BRITISH COUNCIL for a grant to cover the costs of the revision of the English of my thesis, and to Mrs. W. F. J. CAMERON for revising it.

II. MATERIAL.

This paper is based on investigations of the forebrain of Protopterus, Epiceratodus, some Urodeles and Anurans. For comparative purposes I have also studied series of forebrains of Selachians, Ganoids and Teleosts, and some brains of adult Polypterus senegalus, stained by Bielschowsky's method. The material on Protopterus (P. annectens), collected by Dr SVENSSON and the author on McCarthy Island, Gambia, British West Africa, consists of the following specimens:

Protopterus annectens.

Embryonic stages

Stage	No. of spec.	Transv.sect.	Sag.sect.	Hor.sect.
Eggs	11	7	4	
7 mm (7; 7.5)	3	2		1
8 mm (8.3; 8.5)	3	3		
9 mm (9; 9.2; 9.4; 9.5; 9.6)	8	6	1	1
10 mm (10; 10.1; 10.2; 10.3; 10.5)	11	8	2	1
11 mm (11; 11.1; 11.2; 11.5; 11.6; 11.8)	6	6		
12 mm (12; 12.4; 12.5)	5	3	1	1
13 mm (13.6; 13.8; 13.9)	3	3		
14 mm (14; 14.2; 14.3; 14.4; 14.5; 14.8)	11	11		
15 mm (15; 15.5)	4	3		1
16 mm	1	1		
17 mm (17; 17.5)	2	2		
18 mm	1	1		
19 mm (19; 19.5)	2	2		
20 mm (20; 20.2)	2	1	1	
21 mm	1	1		
22 mm (22; 22.5)	2	2		
23 mm (23; 23.5)	2	2		
24 mm (24; 24.5)	2	2		
25 mm	1	1		
27 mm	1	1		
29 mm	1	1		
30 mm	3	2	1	
32 mm	1	1		
35 mm	1	1		
40 mm	1	1		
43 mm	2	1	1	
50 mm	2	1	1	
55 mm	1	1		
60 mm	2	1	1	
95 mm	1	1		

Adult brains

Fixative	Staining	Sectioned	No. of brains
Abs.alk.	Cresylviolet	Transversal	1
Bouin	Azan-Mallory	"	2
10 % neutr.form	Bielschowsky	"	4
"	"	Sagittal	2
"	"	Horizontal	2
Abs.alk.	Cajal	Transversal	1
Bouin	Bodian[1]	"	1
10 % neutr.form	"	"	1
Abs.alk.	"	Sagittal	3
"	"	Horizontal	1
10 % neutr.form	"	"	1
"	Smith-Quigley[2]	Sagittal	1
	Weigert	Transversal	1
	"	Horizontal	1
	Golgi	Transversal	4
	"	Sagittal	3
	"	Horizontal	3

[1] Bodian 1936, 1937. [2] Smith-Quigley 1937.

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As a result of the abundant material it has been possible to make a large number of slides at the same and adjacent stages, especially of younger embryos, and I have thus been able to distinguish in the slides what could be considered as artefacts or individual variations. The embryonic material has been fixed either in BOUINS fluid or in 10 % neutral formol and stained with AZAN-MALLORY. I have also used the Bodian method at different stages of development. I should mention that the methods used to show the myelinisation in the forebrain of the adult brains (WEIGERT, SMITH-QUIGLEY) give very poor results in this brain part, even though other parts of the dipnoan brain stain very well. The myelinisation seems to be restricted chiefly to systems belonging to the lateral forebrain bundle. As a result of the scantiness of living material at my disposal in the Zootomical Institute, my supply of Golgi-preparations is unfortunately rather unsatisfactory. In the brains prepared by this method some parts are rather well impregnated; others, however, are more or less unstained or covered with precipitations. The fibres are, therefore, often disconnected for distances varying considerably in length.

The Epiceratodus material consists of the following specimens:

Epiceratodus Forsteri.

Embryonic stages

Stage	No. of spec.	Transv.sect.	Sag.sect.	Hor.sect.
Eggs	5	3		2
6 mm (6.5)	1			1
7 mm (7; 7.5; 7.6)	3	2		1
8 mm (8; 8.5; 8.6; 8.8)	4	3		1
9 mm (9; 9.3; 9.8)	3	1		2
10 mm (10; 10.4; 10.6; 10.7; 10.8)	7	7		
11 mm (11.5)	1	1		
12 mm (12; 12.5; 12.6; 12.7)	4	4		
13 mm (13.5)	1	1		
14 mm (14.5)	1	1		
15 mm	1	1		
16 mm (16; 16.5)	2	2		
28 mm (28.5)	1	1		
34 mm (34.5)	1	1		
38 mm (38.5)	1	1		
43 mm (43.5)	1	1		
45 mm (about)	1	1		
52 mm	1	1		

Adult brains.

Two series stained by BIELSCHOWSKY's method.

Urodeles.

Triturus vulgaris	25	specimens	between	eggs and 24 mm
Hynobius retardatus	9	„	„	10.8 and 33 mm
Necturus maculatus	9	„	„	10.5 and 30 mm

I have also investigated incomplete developmental series of Triturus cristatus, Siren lacertina, Amphiuma means, Megalabatrachius and Amblystoma.

Anurans.

Pelobates fuscus	14	specimens	between	5 and 14 mm
Xenopus laevis	40	„	„	eggs and metamorphosis
Bufo vulgaris	12	„	„	5 and 13 mm
Rana spec.	40	„	„	eggs and 21 mm

In the amphibian material I have also had at my disposal a large number of adult brains of Rana and Triturus, prepared both for fiber-anatomical and cyto-architectonical studies.

III. THE ONTOGENETIC DEVELOPMENT OF TELENCEPHALON IN DIPNOI, URODELA AND ANURA.

DIPNOI.

Protopterus annectens.

Stage 1.
(Egg; Stage XXV, Kerr 1909)

The description of this stage is based on a specimen which represents the youngest individual, having a fully developed cavity in the rostral part of the originally solid brain rudiment.

In this neural tube there exists a plica encephali ventralis (*pl.v.*, fig. 1 A—B), which marks in the floor the caudal extension of the common di-telencephalic primordium (prosencephalon). Dorsally the lateral walls of the prosencephalon bulge out, forming two caudally pointing lobes (*h.*, fig. 1 A, D), which are bounded by a distinct groove (*s.d.t.*, fig. 1 A, C—D). Ventrally to these lobes lies the yet hollow stem of the optic evagination (*N.opt.*, fig. 1 A), and immediately rostrally to this a fine nerve penetrates the brain wall. The fibres of this nerve are dispersed over a narrow part of the wall extended in a dorso-ventral direction (*N.t.* + *N.olf.*, fig. 1 A—B). The fibres are especially numerous in the dorsal and ventral parts of this area. This nerve constitutes a common rudiment of the terminal and olfactory nerves.

A sagittal section through the rostral parts of the embryonic brain in this stage shows a rather thick floor, which has a well marked depression in its rostral half (*r.po.*, fig. 1 B). The frontal wall and the roof are thinner and in the latter there is another depression, which lies almost vertically above the corresponding structure in the floor (fig. 1 B). In the ventricular wall there is a transverse groove which connects these two depressions (*s.d.v.*, fig. 1 B,

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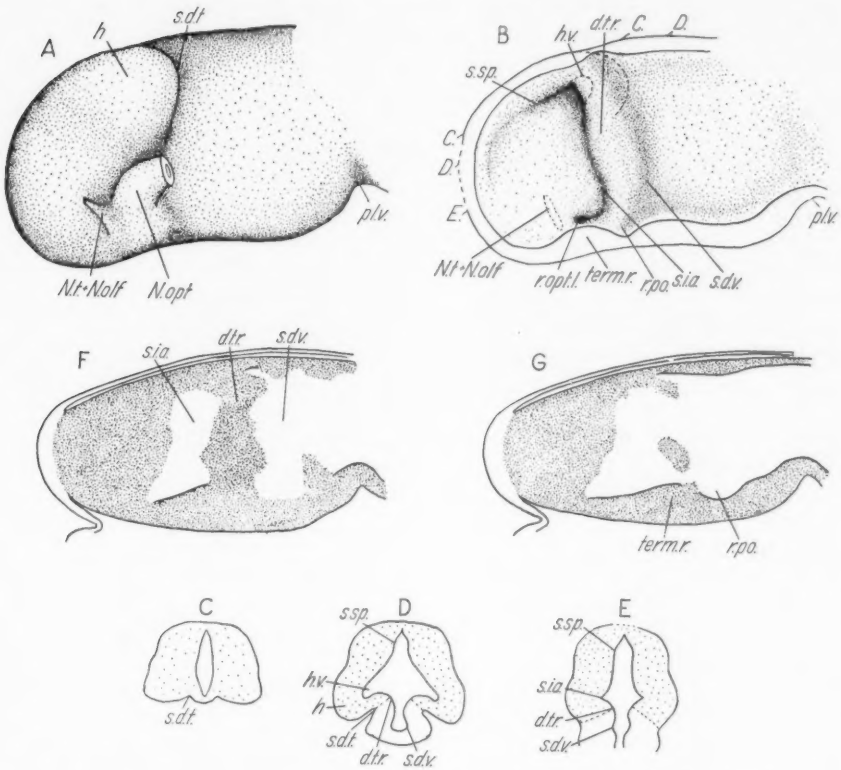

Fig. 1. *Protopterus annectens.* Stage 1 (not hatched). A lateral, B medial view of prosenceph. wall. C—E oblique front. sect., in B indicated by the letterings C—E. F parasagittal, G sagittal sect. through a slightly younger specimen. Dotted areas in C—E indicate telencephalic primordium. A—B graph. rec. 48x; C—E 24x; F—G 48x.

D—E). Somewhat rostrally to the ventral depression, the stem of the optic evagination (*r.opt.l.*, fig. 1 B) opens into the prosencephalic ventricle. The caudally directed evaginations in the dorsal parts of the prosencephalon, which constitute the origin of the future hemispheres, contain a little pocket (*h.v.*, fig. 1 B, D), which is connected with the opening of the optic evagination by a distinct dorso-ventral groove (*s.i.a.*, fig. 1 B, E). This pocket marks the first appearance of the lateral ventricles of the adult brain, and their openings into the prosencephalic ventricle represent the foramen Monroi, which in this stage has a dorso-ventral extension. Another groove starts at the dorsal corner of this foramen, and follows the ventricular wall in a rostral direction (*s.s.p.*, fig. 1 B, D—E).

The groove which connects the optic evagination with the future lateral ventricle, corresponds to the sulcus intraencephalicus anterior of v. KUPFFER (v. KUPFFER 1906). The groove connecting the depressions in the

floor and the roof (*s.d.v.*, fig. 1 B, D—E) corresponds to the sulcus diencephalicus ventralis in Epiceratodus (see BERGQUIST, fig. 150). The subpallial parts of the telencephalon develop in later stages in an area which at this stage contains the sulcus which enters the dorsal corner of foramen Monroi (*s.sp.*, fig. 1 B). I shall, therefore, call this groove *sulcus subpallialis*.

In Stage 1 the floor immediately ventral to the optic evagination is very thick (*term.r.*, fig. 1 B), and this structure corresponds to JOHNSTON's "terminal ridge" (JOHNSTON 1909 b). Later on this ridge contains the optic chiasma. The depression in the floor behind the terminal ridge is thus a recessus postopticus (*r.po.*, fig. 1 B). Between sulcus intraencephalicus anterior and sulcus diencephalicus ventralis the ventricular wall bulges out to form a dorsoventrally extended ridge (*d.t.r.*, fig. 1 B, D—E). A parasagittal section through the primitive forebrain of a somewhat younger specimen shows this (fig. 1 F), and it seems to constitute a dorsal continuation of the terminal ridge. The foremost part of the embryonic brain in this earlier stage is not clearly separated from the skin, and in Stage 1 also there is a trace of this contact (in fig. 1 B indicated by a broken line).

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Stage 2.

(Newly hatched; Stage XXIX—XXX, KERR 1909)

The plica encephali ventralis is deeper and the prosencephalon has curved down ventrally (figs. 1—2). The hemispheres have grown out, chiefly caudally, but they are also beginning to bulge out somewhat in front of the roof and frontal wall of the prosencephalon. The lateral ventricles have increased but are still wholly confined to the caudal parts of the embryonic hemispheres (fig. 2 B).

The depression in the roof of the prosencephalon, described in Stage 1, now forms a shallow but wide evagination, which is a primordium for both the epiphysis and the saccus dorsalis (*ep.* + *sacc.d.*, fig. 2 B). Immediately in front of this primordium the roof bulges into the prosencephalic ventricle, giving the first hint of a velum transversum (*v.t.*, fig. 2 B). On this specimen the frontal wall is rather thick, and still in contact with the skin, at the point indicated in fig. 2 B by a broken line. Ventrally to this contact the frontal wall passes over into the floor, which is rather thin rostrally to the chiasmatic ridge (terminal ridge). Caudally to this ridge lies the recessus postopticus, which is connected by the shallow evagination in the roof by means of a sulcus diencephalicus ventralis (*s.d.v.*, fig. 2 B, F). Immediately in front of the chiasmatic ridge lies the opening of the optic evagination (*r.opt.l.*, fig. 2 B; recessus opticus, KINGSBURY 1895; recessus opticus lateralis, HERRICK 1933 a). Here starts a dorsally directed sulcus intraencephalicus anterior, which enters the ventral corner of the foramen Monroi (*s.i.a.*, fig. 2 B). From this corner

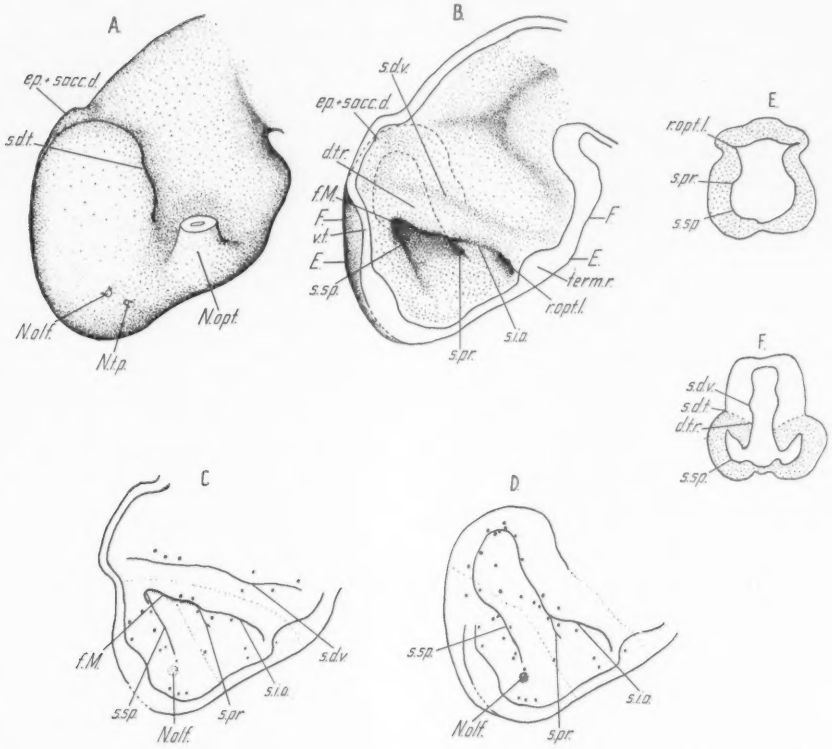

Fig. 2. *Protopterus annectens.* Stage 2 (Newly hatched). A—B, E—F as in fig. 1. C—D the position of the mitoses in the ventricular wall. A—D graph. rec. 46⅔x; E—F 23⅓x.

starts another short groove (*s.pr.*, fig. 2 B, E), which during ontogeny develops into the sulcus preopticus of the adult brain. As in the preceding stage sulcus subpallialis enters the dorsal corner of foramen Monroi (*s.sp.*, fig. 2 B, E) and is connected with the sulcus intraencephalicus anterior by means of the boundary groove of the lateral ventricle (fig. 2 B). The ridge between sulcus diencephalicus ventralis and the sulcus intraencephalicus anterior is conspicous (*d.t.r.*, fig. 2 B, F).

Figs 2 C—D show the position of the mitoses in the ventricular wall, and after studying a great many of such reconstructions, it is evident that the majority of mitoses are located around the three grooves, which are characteristic of the rostral parts of prosencephalon, i. e. sulcus subpallialis, sulcus intraencephalicus anterior and sulcus diencephalicus ventralis. These three sulci constitute "Proliferationsfurchen" (BERGQUIST 1932) and the rostral half of the prosencephalon therefore contains three proliferation zones ("Grundgebiete", BERGQUIST) grouped around the three grooves. These zones extend

dorso-ventrally and the dorsal parts of the first two have been evaginated, and in this stage build up the embryonic hemispheres (fig. 2 C—D).

The caudal proliferation zone, which contains sulcus diencephalicus ventralis, gives rise to the pars frontalis thalami of the diencephalon (BERGUIST 1932). The ridge between sulcus intraencephalicus anterior and sulcus diencephalicus frontalis (*d.t.r.*, fig. 2 B, F) is almost free from mitoses and constitutes a boundary between the proliferation zones around these two grooves. As the zone around sulcus intraencephalicus anterior gives rise exclusively to telencephalic centers, I have called this boundary ridge the *di-telencephalic ridge*. It runs from the chiasmatic ridge up to the velum transversum. Corresponding to this ridge, there exists in the lateral prosensephalic wall a sulcus di-telencephalicus (*s.d.t.*, fig. 2 A, F). Dorsally this sulcus forms a caudal boundary to the hemispheres.

The entrance of the nervous olfactorius (*N.olf.*, fig. 2 A, C—D) is located in the ventral parts of the proliferation zone around sulcus subpallialis.. The more ventral fibres of nervus terminalis now constitute, in contrast to Stage 1, a free root (*N.t.p.*, fig. 2 A).

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Stage 3.
(10.1 mm; Stage XXXII, KERR 1909)

On the lateral wall of the prosencephalon the hemisphere now forms a rounded rostro-caudally extended eminence (fig. 3 A). Rostrally and dorsally it protrudes in front of the frontal wall and roof of prosencephalon (fig. 3 B). The epiphysis and saccus dorsalis are now beginning to develop out of the evagination in the roof (*ep.*, *sacc.d.*, fig. 3 B) described in the preceding stages, and velum transversum is more accentuated (*v.t.*, fig. 3 B), and forms a sac-like invagination into the prosencephalic ventricle. The frontal wall is still rather thick, and just caudal to the point where it passes over into the floor, commissural fibres belonging to the anterior commissure begin to appear (*c.a.*, fig. 3 B, F). The part of the floor which contains these fibres is slightly thicker than the frontal wall immediately in front of it and constitutes a comissural ridge. Between this and the chiasmatic ridge the floor is very thin and forms a wide but shallow depression. In the adult brain this has developed into the very deep recessus preopticus, which is such a characteristic feature in the dipnoan forebrain. The chiasmatic ridge now also contains comissural fibres (*ch.*, fig. 3 B).

Immediately rostral to the velum transversum is a dorsal evagination, which marks the beginning of the paraphysis (*par.*, fig. 3 B). The part of the frontal wall situated between velum transversum and the chiasmatic ridge, contains both a lamina supraneuroporica and a lamina terminalis. It is impossible to fix a distinct boundary between these two in Protopterus as no recessus neuro-

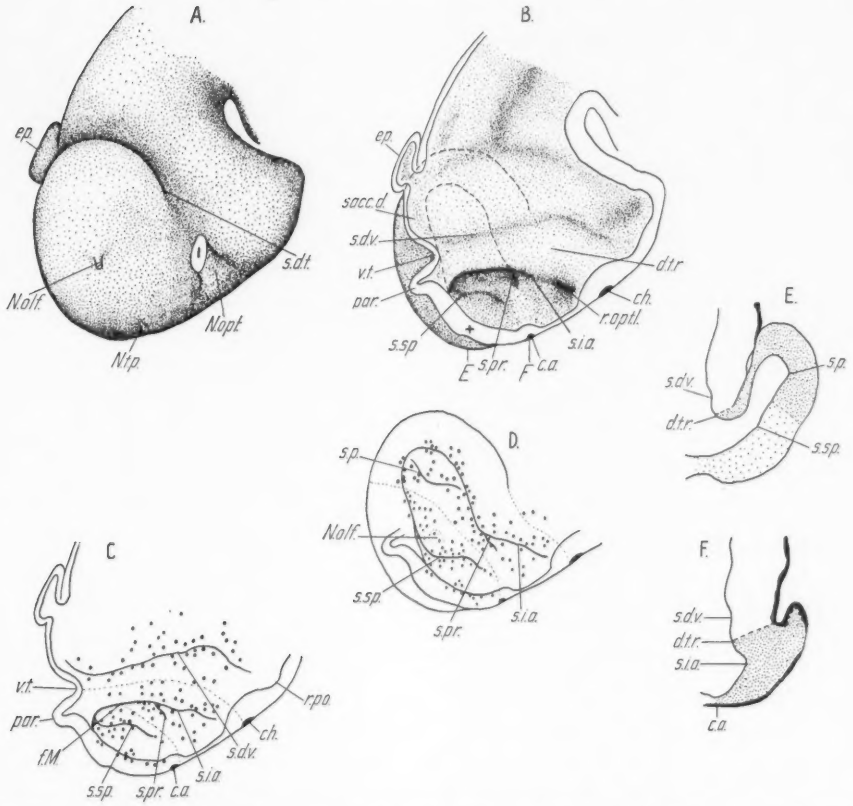

Fig. 3. *Protopterus annectens*. Stage 3 (10.1 mm). Black areas indicate fibres layers. Densely dotted area in E—F marks the caudal telenc. profil. zone; sparsely dotted the subpallial zone. Otherwise as in fig. 2. A—D graph. rec. 47x; E—F 30x.

poricus exists. In preceding stages this boundary could be drawn approximately at the part of the frontal wall which was in contact with the skin. At this stage there is no such contact, but in fig. 3 B the point where the distance between the skin and the frontal wall is shortest is marked by a +, and the boundary ought to be placed in this region.

As in preceding stages the di-telencephalic ridge (*d.t.r.*, fig. 3 B, E—F) is situated between the velum transversum and the chiasmatic ridge, and is bounded rostrally and caudally by sulcus intraencephalicus anterior and sulcus diencephalicus ventralis respectively (*s.i.a.*, *s.d.v.*, fig. 3 B, C—D, F). Judging from the position of the mitoses these two sulci constitute distinct proliferation grooves (fig. 3 C—D). The same applies to sulcus subpallialis (*s.sp.*, fig. 3 B, C—D), the most dorsal part of which has, as a result of the increased hemispheric evagination, been drawn into the lateral ventricle. The foramen Monroi now reaches the lamina supraneuroporica (*f.M.*, fig. 3 C), but the lateral

ventricle is still confined to the part of the hemisphere which lies caudally to this foramen (fig. 3 B).

As in preceding stages there is a short sulcus preopticus, which starts from sulcus intraencephalicus anterior at the point where the latter enters the ventral corner of the foramen Monroi (*s.pr.*, fig. 3 B). In the evaginated part of the proliferation zone situated around the sulcus intraencephalicus anterior (caudal telencephalic proliferation zone), and building up the caudal parts of the hemisphere, there now appears a new proliferation groove (*s.p.*, fig. 3 D, E). As the dorsal part of the zone in question gives rise during the development to the pallium, I shall call this groove *sulcus pallialis*.

The entrance of the olfactory nerve has, as compared with the preceding stages, moved in a dorso-caudal direction, but is still placed in the subpallial proliferation zone (*N.olf.*, fig. 3 A, D).

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Stage 4.
(12.4 mm; Stage XXXIV, KERR 1909)

The hemispheres have already increased rostrally and caudally, but are now also expanding dorsally (fig. 4 A). Through the increasing hemispheric evagination the lateral ventricles have expanded, and are beginning to penetrate into the rostral and ventral parts of the hemispheres.[1] The epiphysis and the saccus dorsalis are well developed, and a deep velum transversum (*v.t.*, fig. 4 B) now lies rostrally to the latter. The paraphysis has the form of a tube-like dorso-rostrally directed evagination (*par.*, fig. 4 B). The part of the lamina terminalis which contains the anterior commissure (*c.a.*, fig. 4 B) has developed into a well marked ridge, "torus transversus" (v. KUPFFER 1906).

Sulcus diencephalicus ventralis and the di-telencephalic ridge are as in the preceding stage. Two grooves now extend from recessus opticus lateralis (*r.opt.l.*, fig. 4 B) to the ventral (caudal) corner of the foramen Monroi. The caudal one represents a sulcus intraencephalicus anterior (*s.i.a.*, fig. 4 B, F), the middle part of which is almost obliterated. The rostral groove is the sulcus preopticus (*s.pr.*, fig. 4 B, F), which has extended downwards ventrally, and now enters the recessus opticus lateralis (fig. 4 B).

The caudal telencephalic proliferation zone is divided into dorsal and ventral areas. The dorsal (pallial) area (*II.*, fig. 4 D) lies around two proliferation groves, i.e. the sulcus pallialis (*s.p.*, fig. 4 E), and the boundary groove which marks the dorsal and caudal extension of the lateral ventricle and which is a direct continuation of the intraencephalic sulcus (cf. B in figs 1—4). The ventral area (*III.*, fig. 4 C—D) is situated around sulcus intraencephalicus and sulcus preopticus. During the ontogenetic development the preoptic nucleus differentiates out of this ventral area of the caudal telencephalic proliferation

[1] In fig. 4 A the most rostral part of the hemisphere is indicated by the letters p. a.

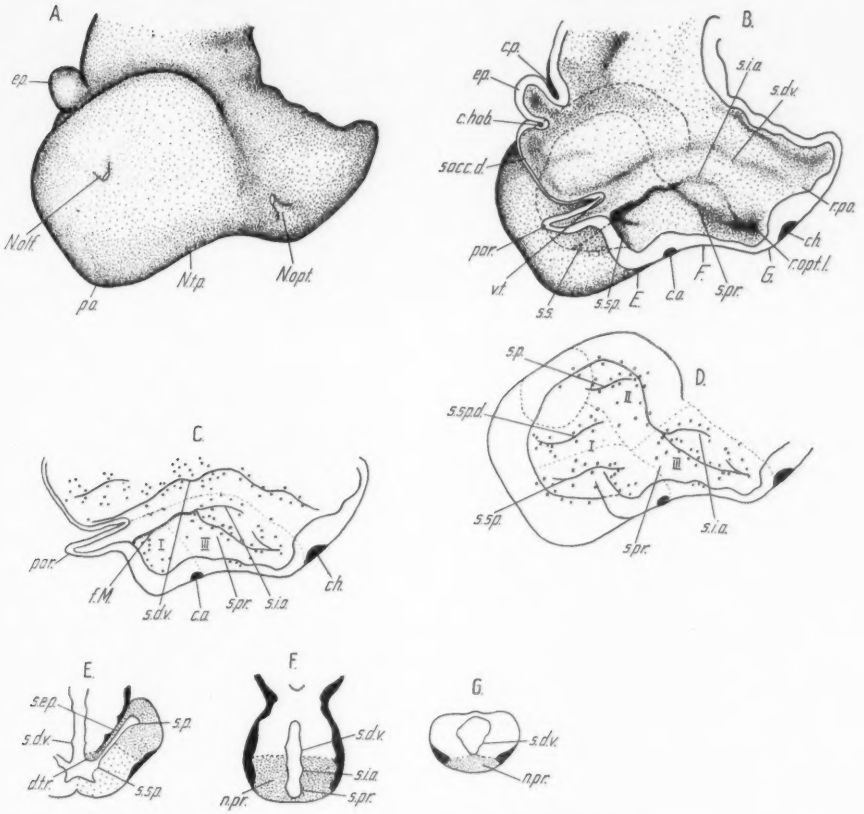

Fig. 4. *Protopterus annectens.* Stage 4 (12.4 mm). Black and dotted areas in C—G as in fig. 3. A—D graph. rec. 45x; E—G 22.5x.

zone. The appearance of fibre layers in the lateral parts of tel- and diencephalon (*n.pr.*, fig. 4 F—G) indicates the outline of this nucleus.

The rostral telencephalic (subpallial) proliferation zone (*I.*, fig. 4 C—D) is situated around the frontal and ventral boundary groove of the lateral ventricle, and around the sulcus subpallialis (*s.sp.*, fig. 4 D—E). In the dorso-caudal parts of this proliferation zone there now exists another proliferation groove (*s.sp.d.*, fig. 4 D), and because of this the subpallial proliferation zone is divided into a dorso-caudal and a ventro-rostral area. There is still, however, no distinct boundary between them.

The entrance of the olfactory nerve has shifted further dorso-caudally (*N.olf.*, fig. 4 A), and it is possible to discern the rudiment of the bulbus olfactorius in the dorso-caudal parts of the hemisphere on the border between the pallial and the subpallial proliferation zones.

The dorsal and caudal parts of the medial walls of the hemispheres are

very thin, and constitute a septum ependymale (*s.ep.*, fig. 4 E). The ventral and rostral parts, however, contain nervous matter and are situated around a short proliferation groove, sulcus septalis (*s. s.*, fig. 4 B), which runs rostrally from the foramen Monroï and merges with the frontal boundary groove of the lateral ventricle. The parts of the medial wall, which in Stage 4 are thickened and contain nervous matter, have been formed as a result of the powerful rostral evagination of the parts of the subpallial proliferation zone which are situated laterally to the lamina supraneuroporica (cf. figs 3 B and 4 B).

Stage 5.
(15 mm; Stage XXXV, Kerr 1909)

The hemispheres have grown considerably in size, especially rostrally. At the same time a very obvious change has occured in the curving upwards of the frontal wall of the third ventricle together with the whole hemispheric rudiment. If a line is drawn connecting the most rostral and caudal parts of the hemisphere, one finds that in stage 5 it is almost parallel to the floor of the preoptic recess, while in the preceding stage it makes an angle of about 60° with the floor. Fig. 5 E—G shows in which way this curving upwards affects the common lamina supraneuroporica-terminalis. The rostral parts of this lamina have curved upwards at right angles to the floor of the preoptic recess in the part which contains the anterior commissure, which lies in this stage, therefore, in the angle between the floor and the frontal wall of the third ventricle. As a result of this curving upwards the foramen Monroi has been compressed and now constitutes an arched opening (fig. 5 E—G). In preceding stages the greatest part of the hemispheric ventricle was situated dorsally and caudally to the foramen Monroi. Because of the increasing evagination most of the ventricle is now situated in front of the foramen.

Compared with the preceding stages the three original proliferation grooves have undergone some changes. Sulcus diencephalicus ventralis, which in stage 4 extended as an unbroken groove from the saccus dorsalis to the postoptic recess, has now only its dorsal part left, and this part (*s.em.th.*, fig. 5 B, G) corresponds to the sulcus eminenthiae thalami of a 16 mm stage of Epiceratodus (Bergquist 1932). From a careful study of a large number of specimens in various degrees of development between stages 4 and 5, it seems to me as if the ventral part of the sulcus diencephalicus ventralis has been shifted ventrally and this displacement, combined with a caudal prolongation of the intraencephalic sulcus, seems to have connected the ventral parts of the ventral diencephalic sulcus with the latter. Fig. 5 E—G tries to illustrate these conditions. In stage 5 we now have an unbroken groove from the ventral corner of the foramen Monroi to the postoptic recess (*s.i.a., s.d.v.*, fig. 5 B). This groove constitutes the sulcus diencephalicus ventralis, and its caudal continuation the sulcus hypo-

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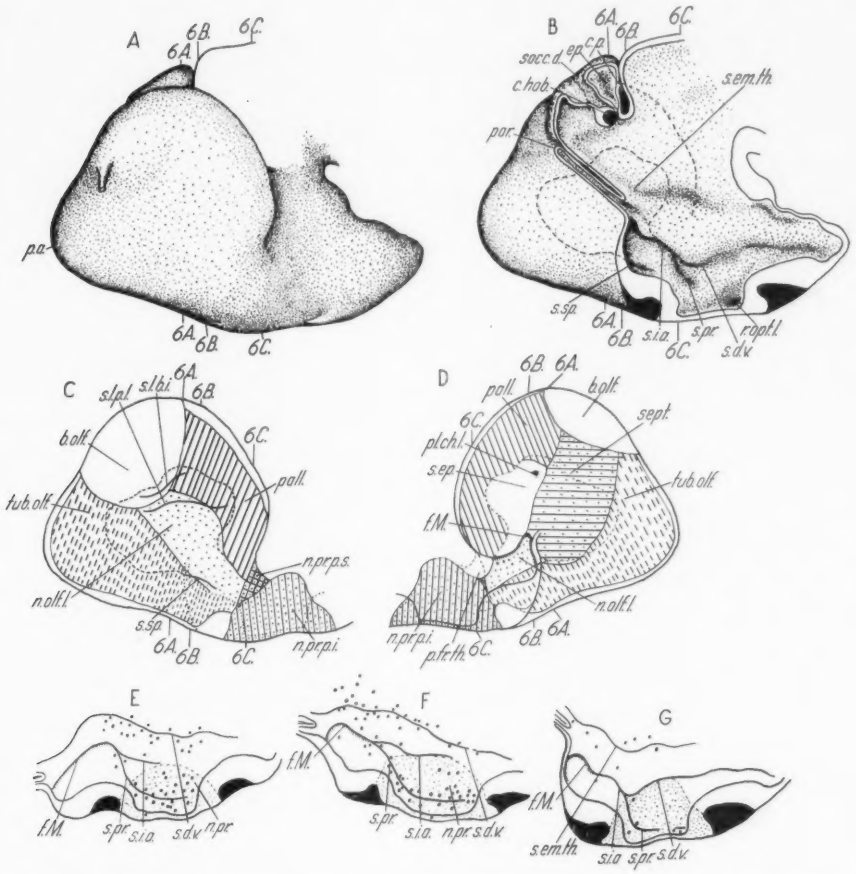

Fig. 5. *Protopterus annectens.* Stage 5 (15 mm). C—D show the extension of telencephalic centers seen in lateral (C) and medial (D) view. E—G position of mitoses and the extension of the preoptic nucleus (dotted area) in three slightly younger specimens. Graph. rec. 44x.

thalamicus of the adult animal. It is possible to make out the boundaries of the preoptic nucleus, and it will be seen that the groove in question lies between this nucleus and pars frontalis thalami (*s.d.v.*, fig. 6 C). The di-telencephalic border now passes from velum transversum, along the caudal arch of the foramen Monroi, the sulcus diencephalicus ventralis, and the caudal boundary of nucleus preopticus down in front of the optic chiasma (fig. 5 G).

The sulcus subpallialis has moved ventrally, and is united with the ventral corner of the hemispheric ventricle. In the part of the telencephalon which has not evaginated in this stage (telencephalon medium) the sulcus subpallialis, dorsally to the anterior commissure, continues a short distance caudally (*s.sp.*, fig. 5 B).

In the hemisphere it now is possible to distinguish the boundary between pallium and subpallium, and in the lateral wall of the hemispheric ventricle this border is marked by a sulcus limitans pallii lateralis (*s.l.p.l.*, figs 5 C; 6 A—B). An investigation of somewhat earlier embryonic stages shows that the proliferation groove in the pallial proliferation zone, sulcus pallialis, moves down ventrally during the ontogenetic development and becomes a boundary groove, the above mentioned sulcus limitans pallii lateralis. In the pallial proliferation zone (dorsal part of the caudal telencephalic proliferation zone; *pall.*, figs 5 C—D; 6 A—C) there now exists a cortical migration (*pall.c.*, fig. 6 B).

The ventral part of the caudal telencephalic proliferation zone has now developed into a nucleus preopticus (*n.pr.p.i.*, figs 5 C—D; 6 C). Between this nucleus and the pallial primordium there exists a transitionary area (*n.pr.p.s.*, figs 5 C; 6 C), which in the adult brain is representated by the pars superior of the nucleus preopticus (see further p. 130).

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In the preceding stage the subpallial proliferation zone was divided into a dorso-caudal and a ventro-rostral area. The former is a primordium of nucleus olfactorius lateralis (*n.olf.l.*, figs 5 C—D; 6 A—B), and there is a trace of its proliferation groove, *sulcus subpallialis dorsalis* (*s.sp.d.*, fig. 6 B). In the specimen representated by stage 5 this groove is very short. In younger specimens it is more conspicous, and in these I have observed a dorsally directed displacement of this groove towards the sulcus limitans pallii lateralis, and in some specimens the rostral parts of this latter sulcus appear to arise from the sulcus subpallialis dorsalis. The ventro-rostral part of the subpallial proliferation zone constitutes a primordium of the tuberculum olfactorium, which gives rise to the basal telencephalic centers, around the ventral corner of the lateral ventricle (*tub.olf.*, figs 5 C—D; 6 A—B).

On the medial side of the hemisphere there is a septum ependymale dorsally to the foramen of Monroi (*s.ep.*, figs 5 D; 6 B). In the dorsal part of this septum there is a small evagination directed into the lateral ventricle; this evagination represents a rudiment of the plexus choroideus lateralis (*pl.ch.l.*, figs 5 D; 6 B). Dorsally and caudally to the septum ependymale are situated the medial parts of the pallial primordium. In front of the septum ependymale the medial hemispheric wall is thickened and contains the septal formation (*sept.*, figs 5 D; 6 A), which borders ventrally the primordium of the tuberculum olfactorium. In the adult brain the septal parts are divided by a sulcus septalis in a dorsal and a ventral area. This sulcus, which in the preceding stage constituted a proliferation groove, has been pushed ventrally into the ventral corner of the lateral ventricle (*s.s.*, fig. 6 A). Thus the part of the septum which is situated dorsally to this corner probably contains only the primordium of pars dorsalis septi. The border between the septal formation

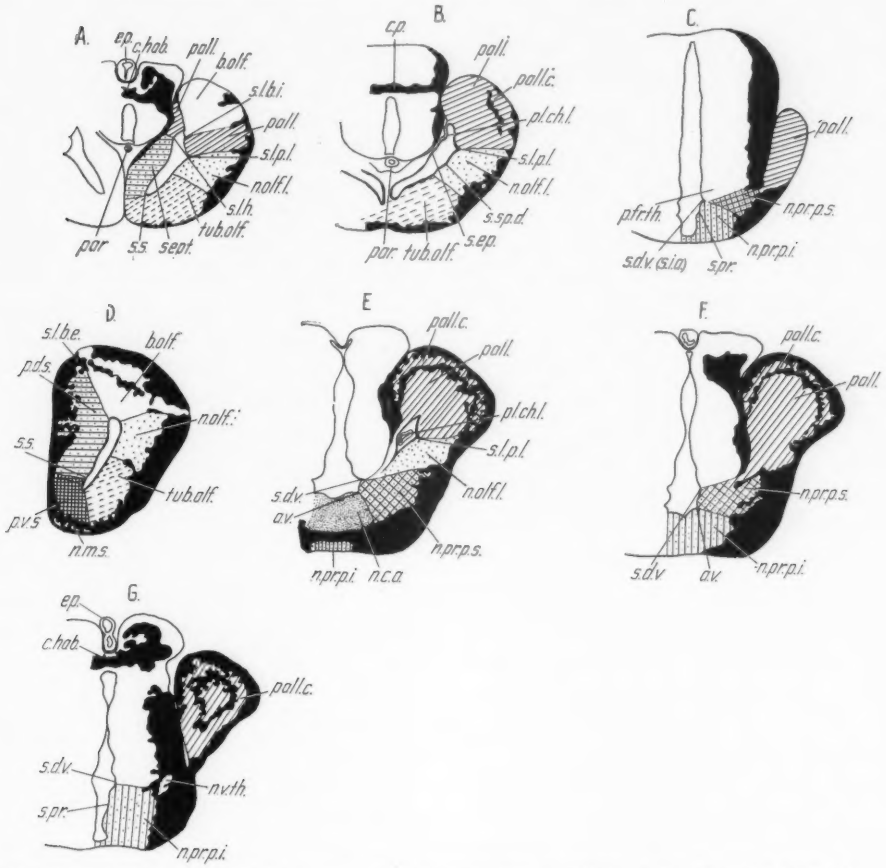

Fig. 6. *Protopterus annectens.* Transv. sect. through the forebrain. A—C Stage 5 (fig. 5), D—G Stage 6 (fig. 7). 30x.

and the medial pallial parts is marked by a short sulcus limitans hippocampi (*s.l.h.*, fig. 6 A).

The bulbus olfactorius is placed dorso-laterally on the hemisphere between the pallium and the subpallium (*b.olf.*, figs 5 C—D; 6 A). In the lateral ventricle the bulbus is bounded by a sulcus limitans bulbii internus (*s.l.b.i.*, figs 5 C; 6 A). As yet there is no distinct exterior boundary groove.

Stage 6.
(29 mm)

Compared with Stage 5 there has been a marked prolongation of the rostral parts of the hemispheres, the primordium of tuberculum olfactorium and the septal formation especially having increased in size (fig. 7 C—D). The caudal

parts of the hemispheres have increased in height and the preoptic recess is deepened (cf. figs 5 B and 7 B). In the ventro-caudal parts of tuberculum olfactorium there now appears a cortical migration (*tub.olf.c.*, fig. 7 C—D). There is no clear demarcation between the rostral parts of this cortex and the ventricular cell-layer of the tuberculum olfactorium. On the lateral hemispheric wall the seat of the caudal parts of the cortex in question is marked in this stage by an indistinct ventro-caudal lobe (*v.c.l.*, fig. 7 A).

In stage 5 the medial parts of tuberculum olfactorium bordered the septal formation in the vicinity of the angulus ventralis of the lateral ventricle (figs 5 D; 6 A). As a result of the deepening of the hemispheres and the lateral ventricle, the sulcus septalis (*s.s.*, figs 6 D; 7 C) is now situated in the medial wall, dorsally to the angulus ventralis, and constitutes a boundary groove between the pars dorsalis and pars ventralis septi, the latter of which now begins to differentiate out of the cell area around the angulus ventralis (*p.v.s.*, figs 6 D; 7 C). Outside pars ventralis in the basal parts of the hemisphere there is a small gathering of cells which have migrated out of the pars ventralis of the septum (*n.m.s.*, figs 6 D; 7 C). Compared with stage 5 the pars dorsalis has increased very much, while the septum ependymale on the other hand is greatly reduced (*s.ep.*, fig. 7 C). The rudiment of the plexus choroideus lateralis, which in the preceding stage consisted only of a small laterally directed pocket, now appears in the form of an ependymal sac., which is to be found in the dorso-caudal parts of the lateral ventricle (*pl.ch.l.*, figs 6 E; 7 C).

The part of lamina terminalis, which contains the anterior commissure, is powerfully thickened (fig. 7 B) and is bounded laterally by a groove (*a.v.*, figs 6 E; 7 B—C), which is the caudal prolongation of the angulus ventralis of the lateral ventricle, or rather the caudal parts of the sulcus subpallialis (see Stage 5 and fig. 5 B—C). This part of the sulcus subpallialis, situated in the telencephalon medium, now constitutes a boundary groove of the lateral parts of the nucleus of the anterior commissure (*n.c.a.*, figs 6 E; 7 C—D).

As in the preceding stage, nucleus preopticus is divided into a ventral area around the sulcus preopticus, pars inferior of nucleus preopticus (*n.pr.p.i.*, figs 6 E—G; 7 C—D; *s.pr.*, figs 6 G; 7 B—C), and a pars superior of the same nucleus (*n.pr.p.s.*, figs 6 E—F; 7 C—D) situated dorso-rostrally to pars inferior. The dorsal border of the common preoptic nucleus is marked by a boundary groove, sulcus diencephalicus ventralis (*s.d.v.*, figs 6 E—G; 7 B—C).

Compared with the subpallial parts the pallium has increased very little. It is still restricted to the dorso-caudal parts of the hemisphere, which are situated caudally and laterally to the foremost diencephalic centers (*pall.*, figs 6 E—G; 7 C—D). They are also, as in the preceding stage, situated behind the foramen Monroi and thus constitute a pars postforaminalis, which, according to HALLER (see p. 10) should not exist in Protopterus.

Laterally to the part of diencephalon which lies dorsally to the pars inferior

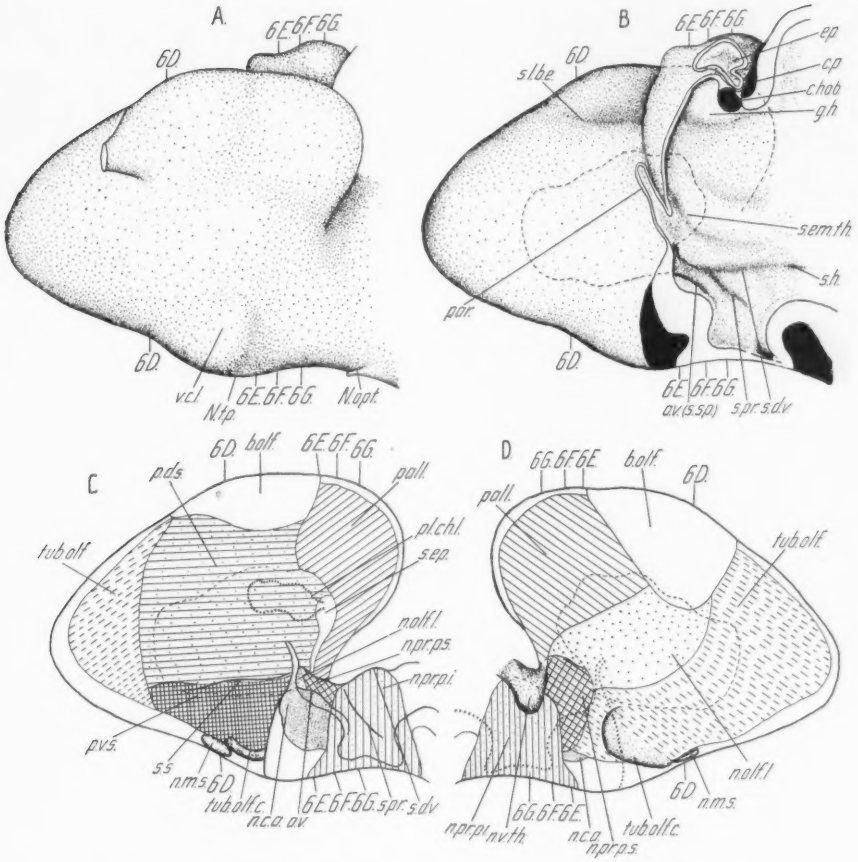

Fig. 7. *Protopterus annectens.* Stage 6 (29 mm). Graph. rec. 43x.

of nucleus preopticus there is a migrated nucleus (*n.v.th.*, figs 6 G; 7 D), the rostral parts of which pass gradually over into the pars superior of nucleus preopticus. This nucleus corresponds to the nucleus ventralis thalami of other lower vertebrates (BERGQUIST 1932; see also p. 117).

The olfactory bulb lies dorso-laterally upon the hemisphere, about half-way between the most anterior and posterior parts of the hemisphere. On the medial side the bulbus is bounded by an exterior groove, sulcus limitans bulbi externus (*s.l.b.e.*, figs 6 D; 7 B).

Stage 7.
(55 mm)

The rostral prolongation of the subpallial parts is very conspicous in this stage (fig. 8), while the foremost parts of the pallium are now also beginning

to appear rostrally to the saccus dorsalis (fig. 8 B). From this stage on this forward growth of the pallium becomes more and more pronounced. At the same time the olfactory bulb is pushed rostrally, and in the adult brain it is situated directly above the most rostral parts of the subpallium (figs 9 A—B; 21 A).

The caudal parts of the pallium, however, as yet build up a lobe situated dorsally and caudally to the foramen Monroi, but as a result of the rostral shifting of the pallial parts, this lobe diminishes during the later ontogenetic development and in the adult brain has disappeared (cf. figs 8 A; 9 A). In the subpallium, however, the ventro-caudal lobe, which is very inconspicous in Stage 6, becomes more and more accentuated, and in the adult brain constitutes a very characteristic structure, which contains the caudal parts of the tuberculum olfactorium ("cortex olfactoria") and the nucleus taeniae (*v.c.l.*, fig. 9 A; *tub.olf.c.*, fig. 29 D; *n.t.*, fig. 29 E).

In the lateral hemispheric wall the boundary between the pallium and the subpallium is marked by the sulcus limitans pallii lateralis (*sl.p.l.*, fig. 8 E). In the medial wall the sulcus limitans hippocampi constituted in Stage 6 the boundary between the pallium and the septum, but in this stage it has been pushed in a dorsal direction and has been united with the dorsal corner of the lateral ventricle. From this stage onwards the medial boundary between the pallial and subpallial parts of the telencephalon is determined ventricularly by this corner. In the septal part of the medial wall the sulcus septalis is very distinct, and its caudal part is heavily ependymated, which is also a characteristic feature of the adult brain. Ventrally to this sulcus the ventricular cell-layer consists of a pars ventralis septi (*p.v.s.*, fig. 8 D), and ventro-laterally to this there exists a nucleus medialis septi (*n.m.s.*, fig. 8 D). The septum ependymale is restricted to a minute area dorsally to the foramen Monroi (*s.ep.*, fig 8 D). The plexus choroideus lateralis, which started in Stage 5 as an evagination from septum ependymale has grown considerable in size, and in the adult brain extends into the most rostral parts of the lateral ventricle.

In telencephalon medium the sulcus preopticus has lost its connection with the sulcus intraencephalicus anterior and now appears as an independent groove in the lateral wall of the deep recessus preopticus (*s.pr.*, fig. 8 B, D). The ventricular cell-layer in this recess is built up by the pars inferior of the preoptic nucleus (*n.pr.p.i.*, fig. 8 C—D, G).

From this stage onwards the subpallial parts, in addition to the continued rostral prolongation, become enlarged ventrally (cf. figs 8 B; 9 B) and recessus preopticus becomes powerfully deepened especially in its caudal parts, and in the adult brain the anterior commissure therefore seems to be situated in the frontal wall of the third ventricle (fig. 9 B).

The bulbus olfactorius is now separated externally from the underlying telencephalic centers by a more or less circle-shaped sulcus limitans bulbi externus (*s.l.b.e.*, figs 8 A; 9 A—B).

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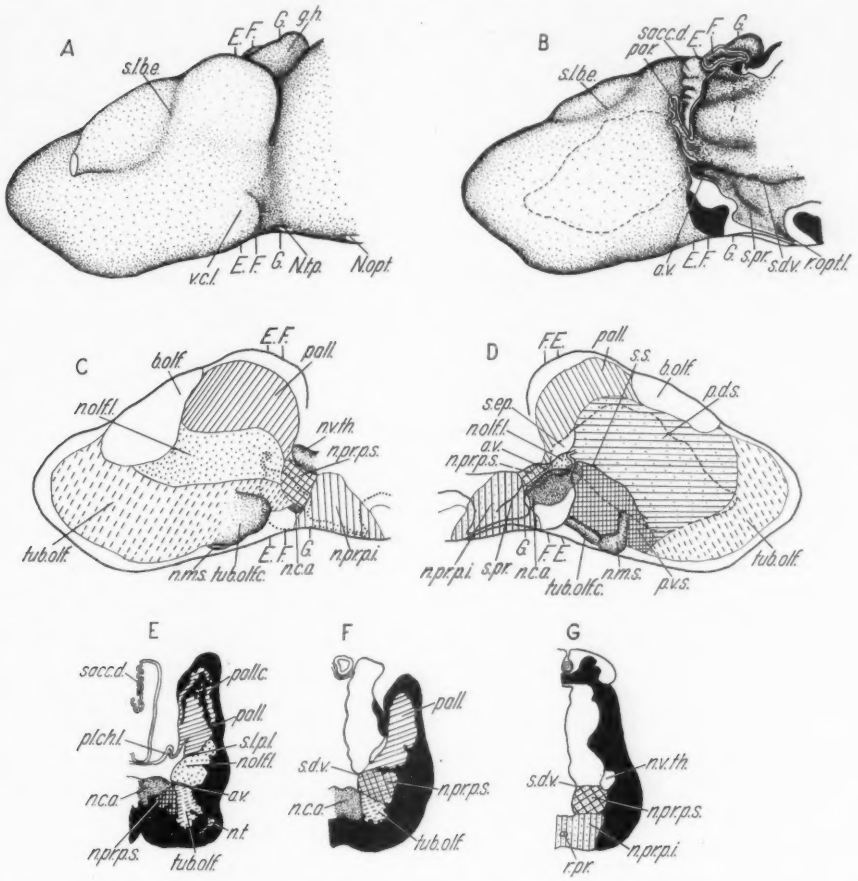

Fig. 8. *Protopterus annectens.* Stage 7 (55 mm). A—D graph. rec.; E—G transv. sect. 22.5x.

Lepidosiren paradoxa.

My Lepidosiren material consists only of two adult brains and I have not, therefore, been able to investigate the ontogenetic development of telencephalon in this animal. KERR (1902), however, has made an investigation of the forebrain ontogeny and, according to his description and figures, the external morphology of Lepidosiren in different stages of development closely follows that of Protopterus. KERR points out that during the ontogenetic development there occurs a displacement of the anterior commissure. "I must again draw attention to the curious differential growth of the anterior part of the floor of the thalamencephalon, which leads to a migration forwards and upwards of the anterior commissure, so that this structure, which at first lay on the

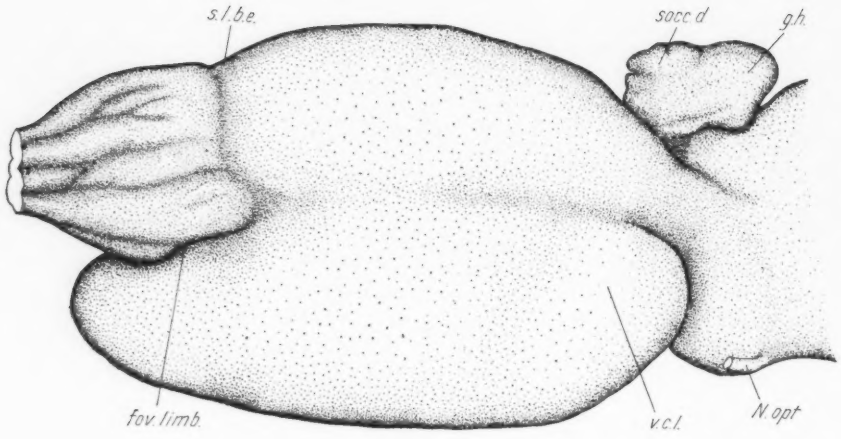

Fig. 9 A.

Fig. 9 A—D. *Protopterus annectens.* Adult forebrain. C—D the extension of telenc. centers in caudal parts of the same; C lateral, D medial view. Graph. rec. A—B 22x, C—D 48x.

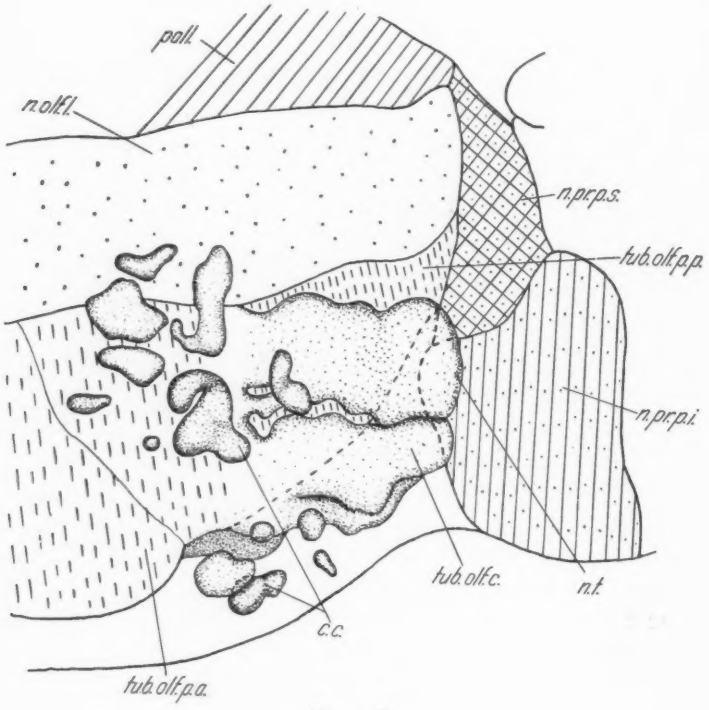

Fig. 9 C.

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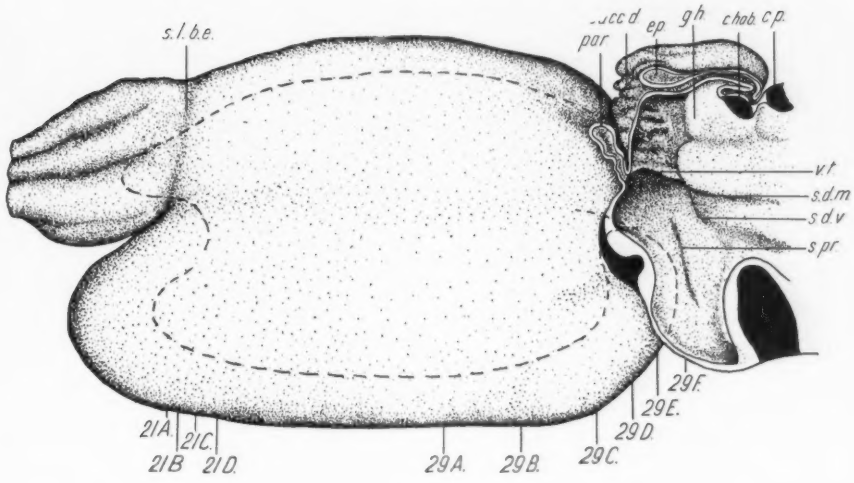
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Fig. 9 B.

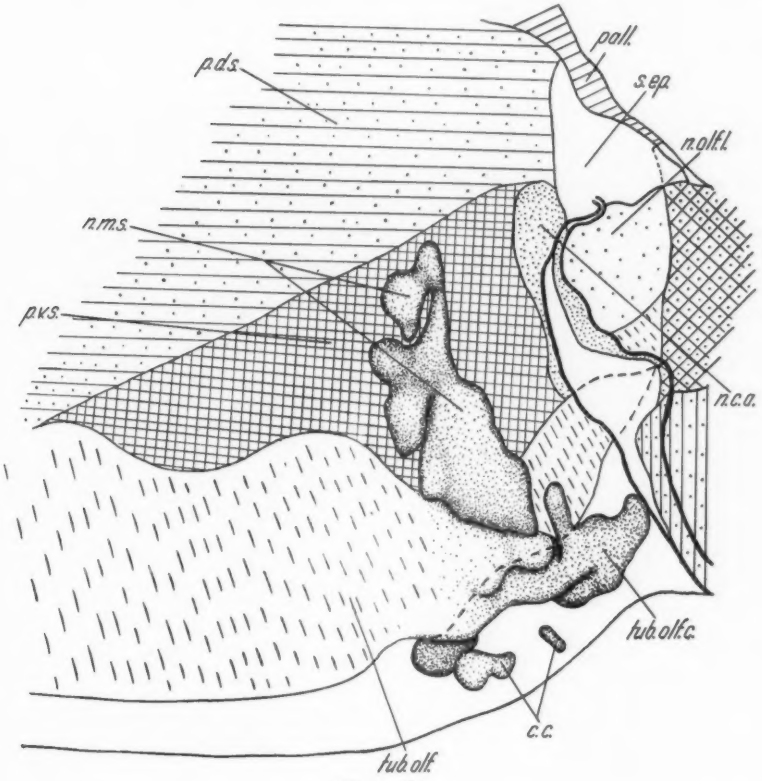
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Fig. 9 D.

floor of the thalamencephalon, comes to be situated well up on its anterior wall." The same conditions also exist, as is evident from the foregoing descriptions (p. 30), in Protopterus. The differential growth in the floor of the thalamencephalon mentioned by KERR seems to depend on the great enlargement of the pars inferior of nucleus preopticus and the chiasmatic ridge, which causes a ventral displacement of the floor of the preoptic recess, mainly in its caudal parts. This, on the other hand, causes the angle between the floor and the frontal wall of the third ventricle to be straightened, and as a result of this the anterior commissure appears to have migrated upwards along the frontal wall of the third ventricle. This impression is accentuated by the powerful development of the ventro-caudal hemispheric lobe (cf. figs 8 B; 9 B).

The rostral prolongation of the hemispheres seems to take place in the same way as in Protopterus. According to KERR "There is no forward growth of the anterior median portion of the wall. The hemispheres soon begin to grow up dorsalwards on either side of the thalamencephalon. Later on there sets in a marked forward growth and the immense antero-posterior length of the hemispheres become in the adult one of their most conspicous features". KERR does not mention the caudal extension of the first evaginated parts of the hemispheres which is typical of Protopterus, but judging from his figures similar conditions exist in Lepidosiren.

KERR has not described the configuration of the ventricular walls and the development of the telencephalic centers, but the external morphology in the two species follows the same lines of development and it is, therefore, very reasonable to suppose that the telencephalic ontogeny of Lepidosiren does not differ in other respects from that which exists in Protopterus. This is also evident from ELLIOT SMITH's investigation (1908) of the telencephalon of the adult Lepidosiren.

Epiceratodus Forsteri.

In the material at my disposal the earliest stages of development are lacking, and in my youngest stage the ventral curving downwards of the prosencephalon is already well pronounced. From GREIL's investigation (1913) it is evident that the embryonic brain, in contrast to the conditions in Protopterus, has a cavity from the beginning, and an anterior neuropore exists. After this has closed, however, no neuroporic recess appears, and it is impossible to draw a distinct boundary between the lamina supraneuroporica and the lamina terminalis, conditions which we have already observed in Protopterus. In this species it was possible to fix this boundary approximately, as we could in this case distinguish the latest contact between the embryonic brain-rudiment and the skin. My Epiceratodus material is too old to make such an observation possible, but according to GREIL the ridge of the future anterior commissure appears

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"in der Region des Neuroporicus anterior". JOHNSTON (1909 b) in his investigations on the anterior end of the brain tube points out that this ridge is situated in the lamina terminalis and the boundary line between the lamina supraneuroporica and the lamina terminalis ought, therefore, in early stages of Epiceratodus to be placed somewhere in front of this ridge, approximately just dorsal to the angle between the floor and the frontal wall of the prosencephalic ventricle as in Protopterus.

In Epiceratodus the hemispheric evagination appears very late compared with the conditions in Protopterus. In this latter species distinct primordia of the hemispheres already exist before the ventral bending down of the primitive forebrain has started. According to GREIL, in Epiceratodus a trace of a dividing up of the primitive forebrain into a telencephalic and a diencephalic part appears first in Stage 41, as in this stage there exists a velum transversum, and the lateral walls dorsal to the optic evagination begin to expand laterally ("Hemisphärenbildung"). According to SEMON (1901) the dividing up of the prosencephalon has already started in Stage 34, but even here the ventral curving downwards is well pronounced, which is evident from GREIL's figures.

The development of the telencephalic centers and grooves has not been described by GREIL, and I will, therefore, give an account of some embryonic stages of the forebrain of Epiceratodus, chiefly with regard to the location of grooves, mitoses and telencephalic centers.

Stage 1.
(Egg; Stage 41, GREIL 1913)

The ventral curving downwards of the prosencephalon is very pronounced, and the floor stands almost at right angle to the caudal parts of the embryonic brain (fig. 10 B). In the roof the epiphysis and saccus dorsalis are rather well developed and in front of the latter a rudimentary velum transversum is invaginated into the prosencephalic ventricle (*v.t.*, fig. 10 B). In the external wall, dorsally to the optic evagination, there is a distinct groove (*s.d.t.*, fig. 10 A), which by means of the fold of the velum passes over to the other side. This groove corresponds to the sulcus di-telencephalicus of Protopterus, which, however, in the latter form starts as two separated grooves which later on become connected dorsally by means of the velum fold. In the floor there are two well developed ridges, an anterior commissural ridge and a posterior chiasma ridge (*c.a.r.*, *ch.r.*, fig. 10 B). Between them there exists a fissure-like depression (recessus preopticus, GREIL 1913). In front of the anterior commissural ridge the lamina terminalis curves up dorsally and constitutes together with the lamina supraneuroporica the frontal wall of the primitive forebrain ventricle. Caudally to the terminal ridge there exists a wide depression in the floor, the rostral part of which corresponds to a recessus postopticus,

and from this a transversal groove, sulcus diencephalicus ventralis, extends up into the primordium of the saccus dorsalis (*s.d.v.*, fig. 10 B—E). In front of this sulcus lies the di-telencephalic ridge (*d.t.r.*, fig. 10 D, E) between the chiasma ridge and the velum transversum. The rostral boundary of this ridge is determined by a sulcus intraencephalicus anterior (*s.i.a.*, fig. 10 B—E). There also exists a transverse sulcus subpallialis (*s.sp.*, fig. 10 B—E) which, together with the sulcus intraencephalicus anterior, ends in a small, laterally directed depression just in front of the velum (fig. 10 B, D). This depression marks the site of the future hemispheric evagination. The location of the mitosis (fig. 10 C) shows that the three transverse grooves in the anterior part of the primitive forebrain constitute proliferation grooves analogous to the conditions in Protopterus. In sulcus intraencephalicus anterior, there exists a short, ventrally directed anterior branch, sulcus preopticus (*s.pr.*, fig. 10 B—C, E). The same condition exists in Protopterus. The caudal proliferation zone, on each side of the sulcus diencephalicus ventralis, is bounded rostrally by the di-telencephalic ridge. In the external wall this boundary is marked by the sulcus di-telencephalicus (*s.d.t.*, fig. 10 A). The two rostral proliferation zones (*I, II*, fig. 10 C) constitute an anterior, dorsally extended section of the primitive forebrain. On the external side this section is penetrated ventrally by the olfactory and terminal nerves (*N.olf., N.t.p.*, fig. 10 A).

My Stage 1 is somewhat younger than the earliest stage described by BERGQUIST (1932). My sulcus diencephalicus ventralis corresponds to the same sulcus in BERGQUIST's description and its caudal continuation, the sulcus hypothalamicus. These two, according to BERGQUIST, constitute a common proliferation groove in the anterior part of the diencephalon, which contains the pars frontalis thalami and the rudiments of the pars dorsalis and pars ventralis hypothalami. In front of this "Grundgebiete" are situated the telencephalic areas, which contain a sulcus intraencephalicus anterior. "Vorn wird das Velum transversum vom Oberteil des sulcus intraencephalicus anterior begrentzt" (p. 221). According to BERGQUIST this groove does not reach the recessus opticus lateralis. Caudally to this recess BERGQUIST indicates a groove as being a sulcus preopticus (*S.praeopt.*, fig. 150; BERGQUIST). From his description and figures, however, it is not evident that this groove reaches the lateral optic recess, which in reality it does, a fact of which I am fully convinced, as I have had at my disposal the specimen (9.3 mm) which was the basis of BERGQUIST's description of his youngest stage. His sulcus preopticus forms in reality the ventral part of sulcus intraencephalicus anterior, a groove which in the 9.3 mm specimen is divided into ventral and dorsal portions as a result of an individual obliteration of the intervening part of the sulcus in this specimen. BERGQUIST's sulcus preopticus does not, therefore, correspond to my sulcus preopticus, which starts as a branch groove of the sulcus intra-

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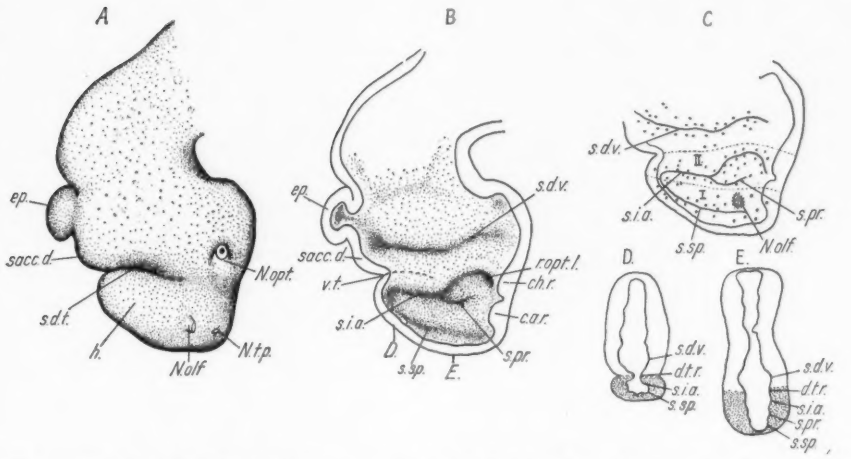

Fig. 10. *Epiceratodus Forsteri.* Stage 1 (not hatched). A—C graph. rec., 44x; D—E transv. sect., dotted areas indicate telencephalic primordium, 22x.

encephalicus anterior. It is situated dorsally and rostrally to the lateral optic recess (*s.pr.*, fig. 10 B), not caudally to this recess as BERGQUIST's is.

According to BERGQUIST the same conditions exist in a 8.5 mm specimen, but in this it is possible to discern a connection between sulcus intraencephalicus anterior and his sulcus preopticus. In the remaining younger embryonic stages of Epiceratodus I have found a distinct unbroken groove, extending from the lateral recess to a point immediately rostral to the velum transversum.

Stage 2.

10.6 mm; Stage 44—45, GREIL 1913)

Compared with the preceding stage the ventral parts of the prosencephalic ventricle have increased rostro-caudally. The frontal wall has been pushed forward and constitutes a wide recess, the roof of which is built up by the almost horizontal dorsal part of the lamina supraneuroporica (cf. fig. 10 B; 11 B). The angle between the horizontal and vertical parts of the lamina supraneuroporica is the site of the future paraphysis (*par.*, fig. 11 B). In front of the now more pronounced velum transversum (*v.t.*, fig. 11 B) the dorsal parts of the telencephalic primordium have been evaginated and now lie laterally and dorsally to the horizontal part of the lamina supraneuroporica (fig. 11 B). The beginning of this hemispheric evagination was indicated by the slight laterally directed depression in the dorsal parts of the telencephalic rudiment in Stage 1. The hemispheric rudiment in Stage 2 contains a lateral ventricle, the boundary groove of which consists of a continuation of the sulcus intraencephalicus anterior (fig. 11 D). The medial wall in this ventricle

is ependymatic along its whole extension (fig. 11 E). The foramen Monroi constitutes a broad opening, which is bounded dorsally by the horizontal section of the lamina supraneuroporica (fig. 11 B—C).

As a result of the hemispheric evagination the dorsal parts of the two telencephalic proliferation zones have been enlarged dorsally. The ventral part of the caudal zone is much broader than in the preceding stage. The sulcus preopticus (*s.pr.*, fig. 11 B—D, G) has been extended ventrally and begins to appraoch the lateral optic recess (*r.opt.l.*, fig. 11 B). The di-telencephalic border is marked by the di-telencephalic ridge (*d.t.r.*, fig. 11 F) between the velum transversum and the chiasma ridge. Both the latter and the anterior ridge now contain commissural fibres.

The entrance of the olfactory nerve has shifted a considerable distance and is now situated on the top of the hemispheric evagination. (*N.olf.*, fig. 11 A). Judging from the specimens represented in Stages 1 and 2 this shifting of the entrance of the olfactory nerve must be very rapid. As result of the scantiness of embryonic material further accentuated by the in some cases, very badly preserved specimens between 7 and 10 mm, I have not been able to make a close study of this process and there is a possibility that the marked ventral position of the entrance of the nerve in stage 1 represents an abnormity. However, in another very young specimen (7 mm) I have observed the entrance of the olfactory nerve lying very close to the terminal nerve at a point closely corresponding to that in Stage 1. These conditions are similar in both hemispheres of the two specimens.

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Stage 3.
(12 mm; Stage 46, Greil 1913)

The anterior recess in the rostral parts of the third ventricle is further accentuated (fig. 12 B). In the angle between the horizontal and the vertical sections of the supraneuroporic lamina there now exists a paraphyseal evagination with a broad opening into the third ventricle (*par.*, fig. 12 B). The evaginated, hemispheric parts of the telencephalon have increased dorsally and rostrally. These parts also contain parts of the lateral ventricle (fig. 12 B).

The sulcus subpallialis is situated in the caudal parts of the subpallial proliferation zone (*s.sp.*, fig. 12 B—C). In the specimen reproduced in fig. 12 A—D there is a short groove anterior to the subpallial sulcus. This groove constitutes a centre for an area of more rapid cell-proliferation, which causes the anterior pushing out of the ventral hemispheric parts. This groove is by no means a constant feature in the embryonic forebrain of Epiceratodus. Its presence varies individually, and where it appears it is of short duration.

In the caudal telencephalic zone of proliferation, it is now possible to distinguish the boundaries of the preoptic nucleus (*n.pr.p.i.*, fig. 12 C—D). The

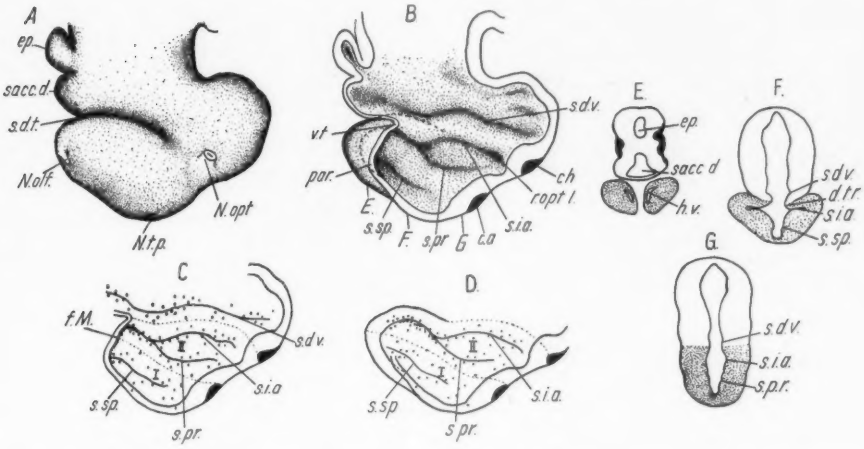

Fig. 11. *Epiceratodus Forsteri.* Stage 2 (10.6 mm). A—D graph. rec., 42x. E—G transv. sect., 21x.

pallial proliferation zone builds up the dorso-caudal parts of the hemispheric evagination. Between this pallial zone and the preoptic nucleus there exists a narrow strip (*n.pr.p.s.*, fig. 12 C—D), which contains the branching off of the preoptic sulcus (*s.pr.*, fig. 12 B—D). This part represents the primordium of the pars superior of the nucleus preopticus.

The sulcus preopticus now enters the lateral optic recess, whereas the intraencephalic sulcus has lost its connection with this recess. The ventral part of this sulcus constitutes a dorsal boundary groove of pars inferior of the preoptic nucleus (fig. 12 C—D).

The primordium of the bulbus olfactorius is situated dorsally on the hemispheric evagination (*b.olf.*, fig. 12 C), and now contains a small ventricle (*b.v.*, fig. 12 C). In a slightly older stage, this ventricle is bounded in the lateral ventricular wall by a sulcus limitans bulbii internus (*s.l.b.i.*, fig. 12 E—G). In this later stage a groove also exists in the dorsal parts of the lateral ventricular wall. This groove seems to be a proliferation groove for the caudal parts of the olfactory bulb and the neighbouring parts of the pallial area. It probably represents an anterior part of a sulcus pallialis, but it is not a constant feature in the forebrain of Epiceratodus (*s.p.?*, fig. 12 E).

Stage 4.
(14.5 mm)

I have described in Protopterus a dorsally directed curving upwards of the hemispheres and the frontal wall of the third ventricle (p. 24). This takes place between Stages 4 and 5. In Epiceratodus also there is a bending up of the anterior parts of the brain, but there is a distinct difference as compared with

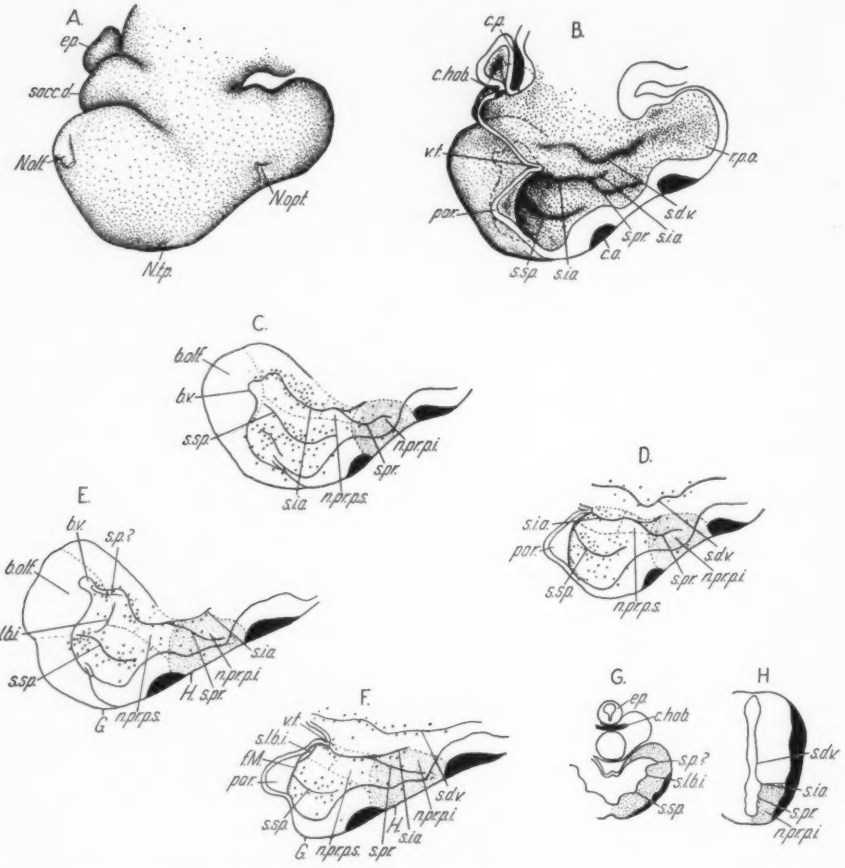

Fig. 12. *Epiceratodus Forsteri.* A—D Stage 3 (12 mm), graph. rec., 44x. E—H 12.5 mm. E—F graph. rec., 44x. G—H transv. sect., 22x.

the conditions in Protopterus. There exists no obvious change in the relationship between the hemispheres, the frontal wall, and the rest of the prosencephalon. The bending up includes all parts of the primitive forebrain, not only its anterior derivatives as was the case in Protopterus. Compare for instance the compressed foramen Monroi in Stage 5 in this latter species with the same structure in Epiceratodus in Stage 4. In the latter no trace exists of such a compression. Furthermore, a straight line passing through the most anterior and posterior parts of the hemispheres in Epiceratodus forms an angle with the floor of the third ventricle; this angle does not undergo any change between Stages 3 and 4. In the corresponding stages in Protopterus (Stages 4 and 5), on the other hand, the line in question is turned until almost parallel to the floor of the third ventricle.

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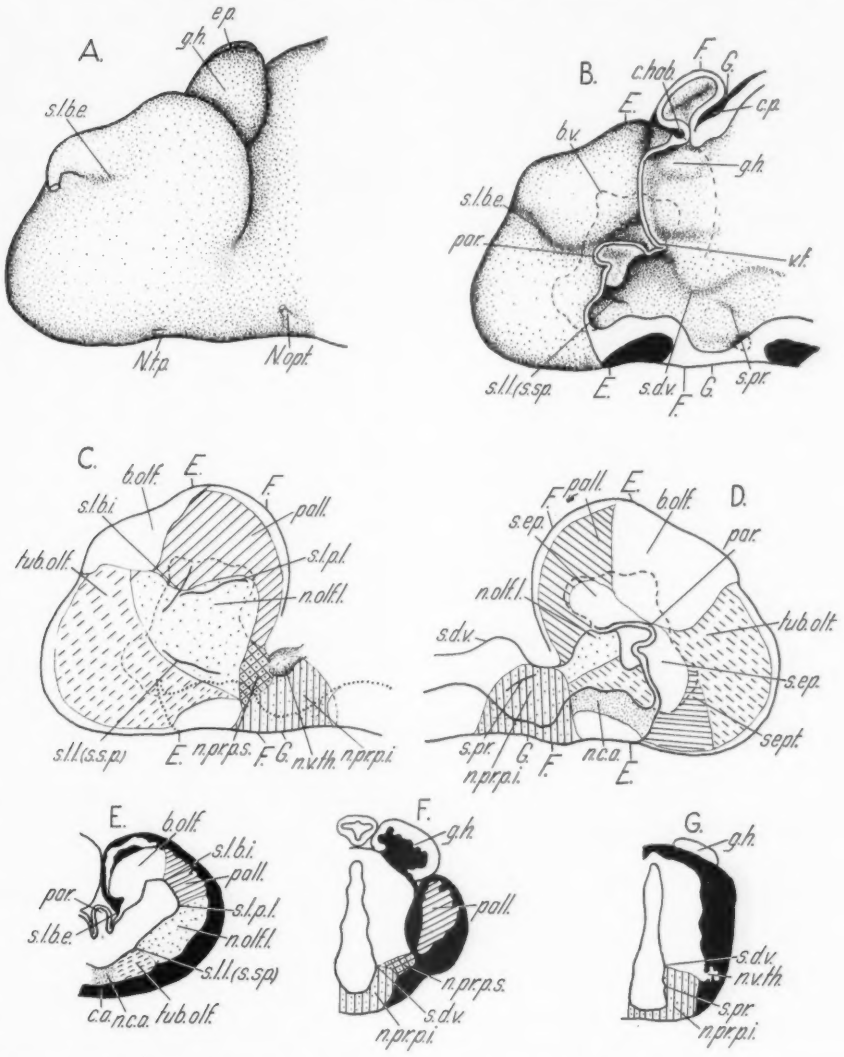

Fig. 13. *Epiceratodus Forsteri.* Stage 4 (14.5 mm). A—D graph. rec. 55x. E—G transv. sect., 45x.

In the present stage of Epiceratodus the hemispheric evagination has increased, and the dorsal parts have grown out caudally forming, as in Protopterus, a pars postforaminalis (cf. figs 12 A—B; 13 A—B). The ventral parts have increased rostrally and, as in Protopterus, the subpallial parts develop more rapidly than the pallial, which are still restricted to the caudal, dorsal parts of the hemisphere. The paraphysis now constitutes a sac-like evagination of the dorsal parts of the supraneuroporic lamina (*par.*, fig. 13 B, E). The foramen

Monroi is dorso-ventrally extended and reaches from the velum down to the foremost parts of the ridge of the anterior commissure. The lateral ventricle contains three pockets, a caudal, dorsally and caudally to the foramen Monroi, a dorso-rostral in bulbus olfactorius, and a ventro-rostral (fig. 13 B). The medial hemispheric wall contains a septum ependymale (*s.ep.*, fig. 13 D), which covers a much greater area than the same structure in the corresponding stage (Stage 5) of Protopterus. It is extended in front of the foramen Monroi, whereas in Protopterus it is restricted to an area caudal and dorsal to this foramen. Ventro-medially to the lateral ventricle there now exists a primordium of the septal formation (*sept.*, fig. 13 D).

In the lateral wall of the hemispheric ventricle there are three grooves. The olfactory bulb is bounded by a sulcus limitans bulbii internus (*s.l.b.i.*, fig. 13 C, E). Caudally to this groove there now exists a sulcus limitans pallii lateralis (*s.l.p.l.*, fig. 13 C, E). Due to the scantiness of my material of older embryonic stages of Epiceratodus, I have not been able to decide whether this groove has developed out of a sulcus pallialis as in Protopterus. I have found this pallial sulcus in only one specimen (described in Stage 3). Probably, the sulcus limitans pallii lateralis appears as a boundary groove, without being preceded by any proliferation groove, which is contrary to the conditions in Protopterus.

In the ventral parts of the lateral ventricle the sulcus subpallialis now constitutes a boundary groove, sulcus limitans lateralis (*s.l.l.* [*s.sp.*], fig. 13 C, E) between the primordia of the tuberculum olfactorium and the lateral olfactory nucleus (*tub.olf.*, *n.olf.l.*, fig. 13 C, E).

There now exists an unbroken groove from the foramen of Monroi down into the hypothalamus (*s.d.v.*, fig. 13 B). This is BERGQUIST's sulcus diencephalicus ventralis (with the sulcus hypothalamicus). I have not been able to decide whether this groove represents only a caudal prolongation of the dorsal parts of the sulcus intraencephalicus anterior or whether the ventral part of the embryonic sulcus diencephalicus ventralis has lost its connection with the dorsal part and been fused with the intraencephalic sulcus. In the preceding stages of Epiceratodus the embryonic sulcus diencephalicus ventralis constitutes a deep and well marked sulcus, and it does not seems probable that its sharply defined ventral part suddenly should disappear. I am of the opinion that the groove, which in older stages and in adult brains of Epiceratodus extends between the foramen Monroi and the hypothalamus, represents the ventral part of the original transverse proliferation groove, the sulcus diencephalicus ventralis, which has been united with the sulcus intraencephalicus anterior.

Bulbus olfactorius is situated dorsally on the hemisphere, but, in contrast to the conditions in Protopterus, its greatest extension lies in the medial hemispheric wall (*b.olf.*, fig. 13 C—E). The external medial border of the olfactory bulb is accentuated by a very deep groove, which continues caudally to the

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bulbus and marks there the external boundary between the pallium and the septum ependymale. The rostral part of this groove constitutes a sulcus limitans bulbii externus (*s.l.b.e.*, fig. 13 B, E).

Stage 5.
(43.5 mm)

Compared with the preceding stage the most conspicous feature is the powerful development of the subpallial parts of the hemispheres. These parts have grown out, not only rostrally but also ventrally, and they contain the now very much enlarged ventral anterior pocket of the lateral ventricle. The pallium is still very small, but is beginning to grow out rostrally (*pall.*, fig. 14 C—D), and now contains a well developed cortical formation (*pall.c.*, fig. 14 F). The rostral prolongation of the pallial parts becomes more pronounced during the subsequent development, and in the adult brain is more advanced than in Protopterus. The olfactory bulb and the rostral parts of the pallium lie in the adult Epiceratodus well in front of, and dorsal to, the anterior subpallial parts (cf, HOLMGREN and VAN DER HORST 1925). In the subsequent stages there also exists a powerful ventral extension of the subpallial parts. This is also the case in the ventral part of the telencephalon medium. This is indicated in Stage 5 by the deepened preoptic recess (cf. figs 13 B; 14 B). As in Protopterus it appears as if these conditions have caused the anterior commissure in the adult brain to be pushed up dorsally along the frontal wall of the third ventricle (see p. 34).

In the subpallial parts the well developed cortex of the tuberculum olfactorium, which is such an outstanding feature in the hemispheres of Protopterus, is absent. There is, however, a tendency to develop such a cortex in Epiceratodus. In the ventrocaudal parts of the tuberculum olfactorium there exists, in the present stage, an area (*tub.olf.c.*, fig. 14 E—F) in which cells and small clusters of cells appear, which are more or less separated from the ventricular layer. These cells probably represent a "cortex olfactoria".

The boundary groove between the tuberculum olfactorium and the lateral olfactory nucleus, the sulcus limitans lateralis (sulcus subpallialis) of the preceding stage, has been obliterated in Stage 5. This is also the case in the adult brain.

In the medial hemispheric wall there exists a sulcus septalis (*s.s.*, fig. 14 E), which separates the primordia of pars dorsalis and pars ventralis septi (*p.d.s.*, *p.v.s.*, fig. 14 D—F). Externally to the latter there appear migrated cells, probably representing the rudiment of a nucleus medialis septi (*n.m.s.*, fig. 14 F). In contrast to the conditions in Protopterus, the septum ependymale (*s.ep.*, fig. 14 D—F) is well pronounced, and it now contains laterally directed diverticles which constitute the origin of the plexus choroideus lateralis (*pl.ch.l.*,

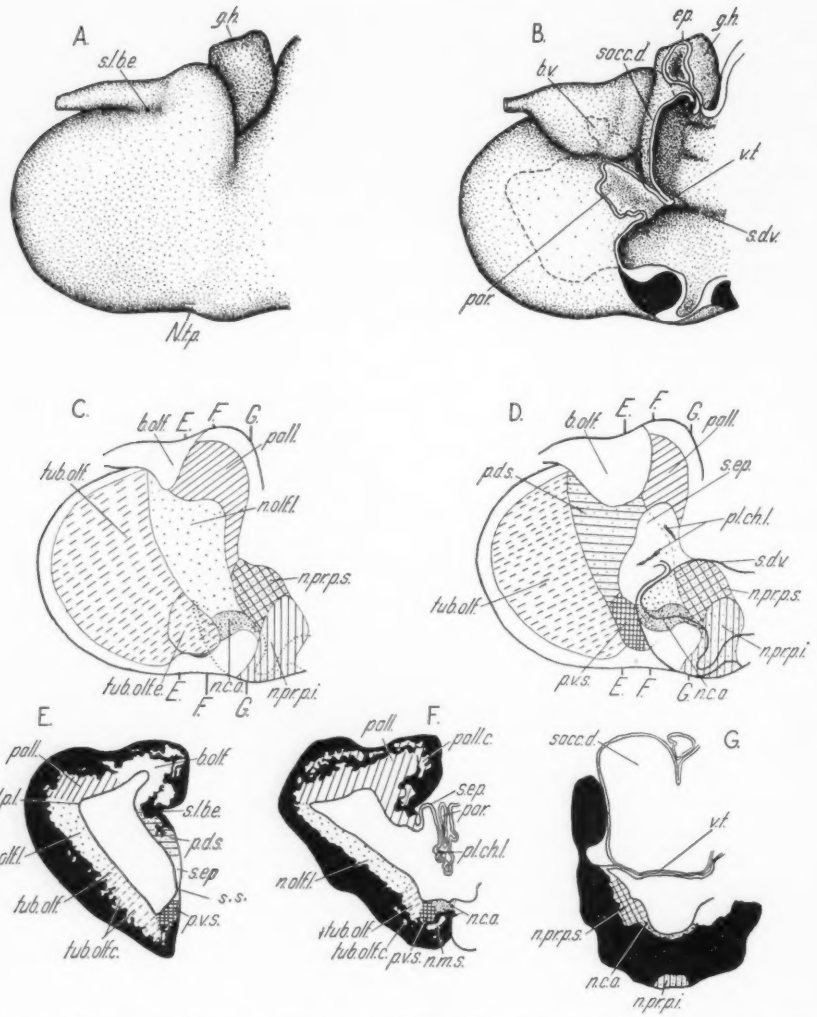

Fig. 14. *Epiceratodus Forsteri*. Stage 5 (43.5 mm). A—D graph. rec., 51x. E—G transv. sect., 48x.

fig. 14 D, F). The conditions in the adult brain show that this ependymatic part of the medial hemispheric wall undergoes enormous development in later ontogenetical stages (see p. 66).

URODELA.

The ontogenetic development of telencephalon in Urodeles is well known thanks to the investigations of v. KUPFFER (Salamandra, Triton, Necturus;

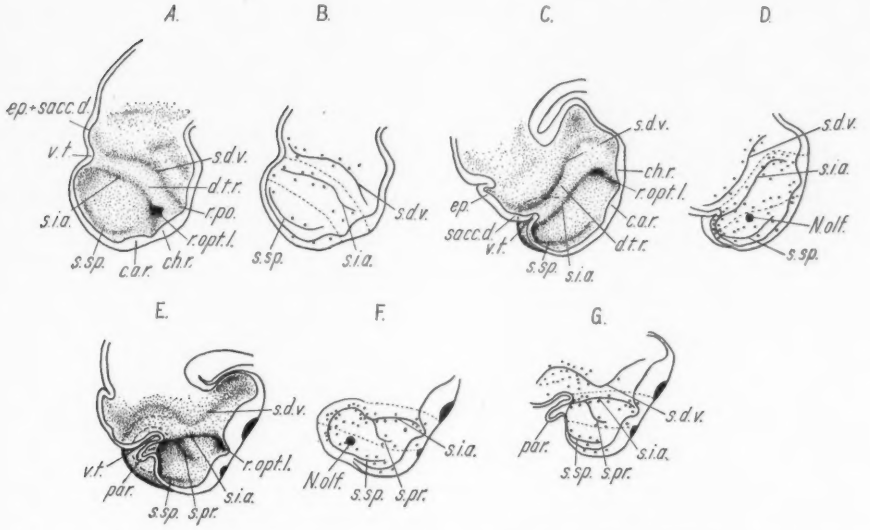

Fig. 15. *Triturus vulgaris*. A—B, C—D and E—G show the prosencephalic wall in three different stages (not hatched). Graph. rec., 44x.

1906), Smith (Desmognathus; 1914), Söderberg (Triton; 1922); Burr (Amblystoma; 1922), Sumi (Hynobius; 1926), Baker and Graves (Amblystoma; 1932), and Herrick (Amblystoma; 1910—39). From these investigations it is evident that telencephalic ontogeny follows the same lines of development in the different species of Urodeles. In early stages the ventral curving downwards of prosencephalon is very conspicous. A distinct recessus neuroporicus does not appear after the closing of the anterior neuropor, and, as in Dipnoi, no distinct boundary exists between lamina terminalis and the supraneuroporic part of the frontal prosencephalic wall. The hemispheric evagination, which does not appear before the ventral bending down of prosencephalon is well pronounced, begins in the dorsal part of the prosencephalic wall adjacent to the supraneuroporic lamina, just in front of the rudiment of the velum transversum (the same conditions as in Epiceratodus). The telencephalic centers differentiate very late in the ontogenetic development, and it is a typical feature of the Urodeles that these centers retain their character of often indistinctly limited primordia even in the adult forebrain. Compared with this, conditions in Dipnoi represent a more advanced stage.

In order to check whether there exists in Urodeles any correspondence to the proliferation grooves and zones in Dipnoi, I have investigated earlier stages of Triturus vulgaris, Hynobius retardatus and Necturus maculatus.

Such an investigation shows that in earlier ontogenetic stages three transverse grooves appear in the anterior part of the ventricular prosencephalic wall. In the immediate vicinity of these the cell-proliferation is more pronounced

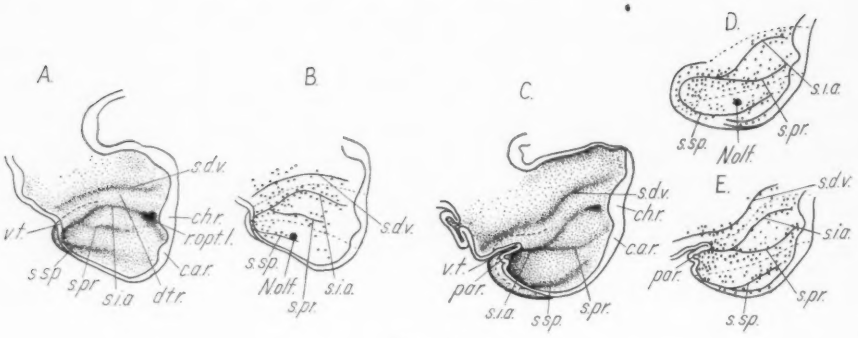

Fig. 16.

Fig. 16 A—L. *Necturus maculatum*. Forebrain in 10.5 mm (A—B), 12 mm (C—D) and 18 mm (F—L). Graph. rec. A—E 16x.; F 24x.; G—L transv. sect. indicated in F by the letterings G—L, 45x.

than in other parts of the ventricular wall. The two more caudal of these grooves, sulcus diencephalicus ventralis and sulcus intraencephalicus anterior (*s.d.v., s.i.a.*, figs 15 A, 16 A), constitute a caudal and a rostral boundary to the di-telencephalic ridge (*d.t.r.*, figs 15 A, 16 A). This ridge extends between the chiasma ridge and the rudiment of velum transversum (*ch.r., v.t.*, figs 15 A, 16 A). The di-telencephalic sulcus in the lateral prosencephalic wall corresponds to the di-telencephalic ridge, and in front of this sulcus there exists a dorso-ventrally extended, oval-shaped swelling out of the lateral wall.

From the position of the mitoses in the ventricular wall (figs 15 B, D, F—G, 16 B, D—E) we can recognize in Urodeles also three zones of proliferation grouped round the three grooves in the anterior part of the prosencephalon. There is a zone with sulcus diencephalicus ventralis as a center, which gives rise to the foremost parts of the diencephalon. Another area lies around sulcus intraencephalicus anterior, and finally one around sulcus subpallialis (*s.sp.*, figs 15, 16). The two last mentioned zones constitute the telencephalic primordium.

A fourth proliferation groove, sulcus preopticus, appears in the caudal telencephalic zone, either very early (Necturus, *s.pr.*, fig. 16 A—B) or somewhat later (Triturus, *s.pr.*, fig. 15 F—G). This groove is connected to the dorsal parts of sulcus intraencephalicus anterior, which in early stages always extends between the optic evagination, recessus opticus lateralis, and a point just in front of the velum transversum. In this part there exists a small depression in the ventricular wall into which both sulcus intraencephalicus anterior and sulcus subpallialis (fig. 15 A) enter. This depression is situated immediately ventrally to lamina supraneuroporica, and is the site of the future hemispheric evagination. When this starts, parts of the lamina are evaginated, and in later stages build up the caudal portion of the medial wall (septum ependymale,

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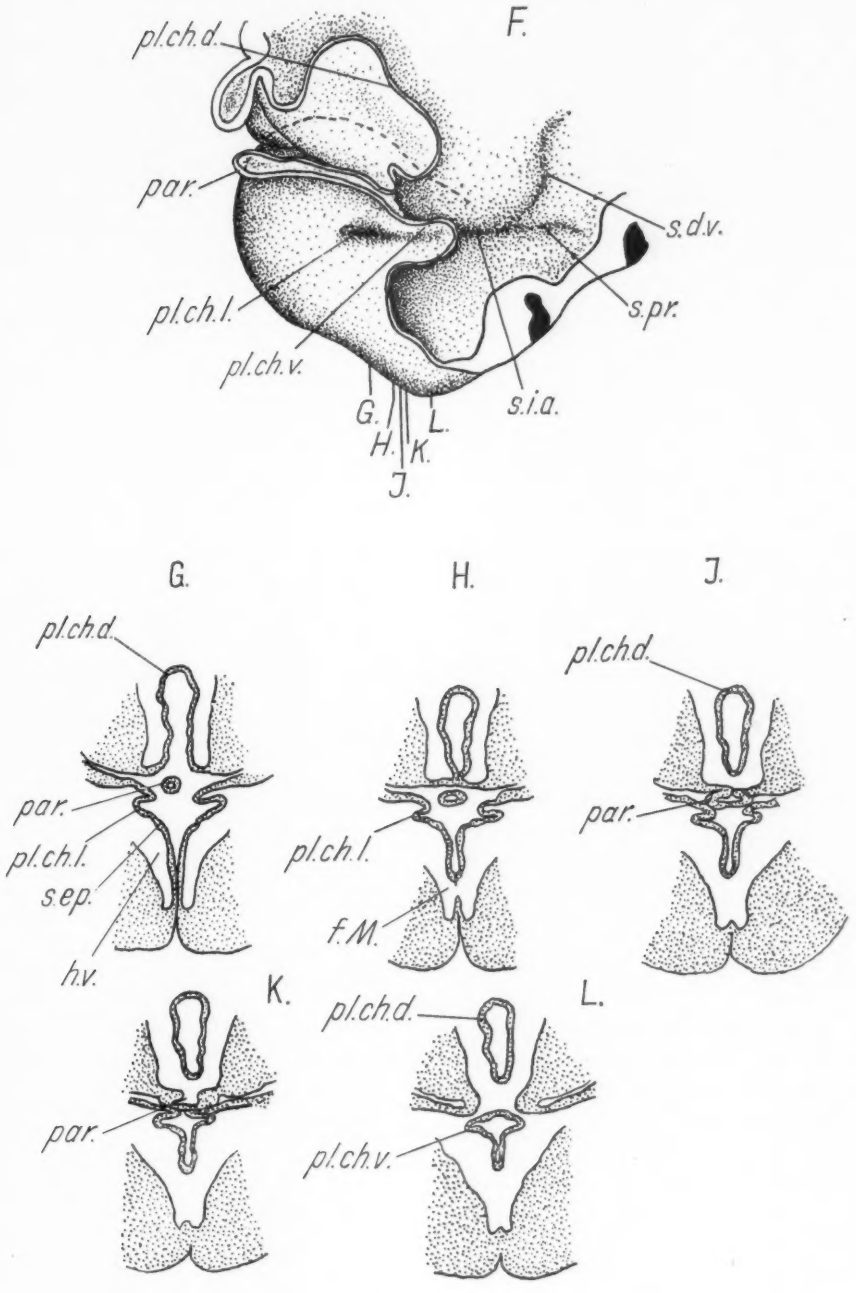
F.
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Fig. 16 F—L.

s.ep., fig. 16 G). To begin with the hemispheric evagination is directed dorsally and includes the border-region between the pallial and subpallial zones of proliferation (figs 15, 16). Later on the evaginated parts begin to expand rostrally, and at the same time the original prosencephalic part of the embryonic brain is bent up dorsally (cf. the position of the floor of the third ventricle in fig. 16 C—F).

The ontogenetic development hitherto described of the forebrains in Urodeles, takes place in exactly the same manner as that already known from the development of Epiceratodus. In later stages, however, there is a difference in as much as the rostral prolongation of the hemispheric primordium is very conspicous in both pallium and subpallium simultaneously. In Dipnoi this prolongation was in the beginning almost entirely restricted to the subpallial parts. The pallial parts also expand caudally, forming a caudal lobe of the hemisphere which, contrary to the conditions in Dipnoans, is very conspicous in adult forebrains.

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During the later ontogenetic development the septum ependymale increases very much in size and folds begin to appear in its rostral parts (*pl.ch.l.*, fig 16 F—H). These develop into a plexus choroideus lateralis. Just in front of foramen Monroi the septum ependymale constitutes the greatest part of the medial hemispheric wall (*s.ep.*, fig. 16 G). When the foramen breaks through, the ependymatic septa of the two hemispheres become united in their ventral parts, and constitute the dorsal boundary of the foramen Monroi (fig. 16 H), and immediately caudally to the opening of the paraphysis the dorsal parts also become fused (fig. 16 K—L). In this way we get an unpaired plexus choroideus ventralis in the ventral part of the third ventricle (*pl.ch.v.*, fig. 16 L). In the development stage when the plexus choroideus lateralis begins to infold from septum ependymale, the latter resembles very closely the same structure in an older stage of Epiceratodus (cf. figs 14 F and 16 H), but in the subsequent development it does not expand rostrally as in the last mentioned species. As is shown above it expands caudally and constitutes the plexus choroideus ventralis. In the third ventricle there also appears another choroidal fold, plexus choroideus dorsalis (*pl.ch.d.*, fig 16 F—L), which originates from a caudally directed infolding of the frontal wall of saccus dorsalis.

Ventrally to the pallial primordium, the caudal telencephalic proliferation zone gives rise to a preoptic nucleus. The dorsal part of this borders an area containing cells and small cell-clusters. These are more or less separated from the ventricular cell-layer of pars frontalis thalami and represent a nucleus ventralis thalami. In Necturus this structure constitutes a well defined nucleus.

The ventral part of the sulcus intraencephalicus anterior (*s.i.a.*, fig. 16 E) loses its connection with the lateral optic recess and becomes fused with the ventral part of sulcus diencephalicus frontalis (*s.d.v.*, *s.i.a.*, fig. 16 C, F). In this way the sulcus diencephalicus ventralis of the adult brain originates (in

the same manner as in Dipnoi). This sulcus constitutes in its rostral parts the dorsal, ventricular boundary of the preoptic nucleus.

In early stages the olfactory nerve enters the forebrain in the subpallial proliferation zone (*N.olf.*, figs 15 D, F, 16 B, D). When the bulbar formation begins to differentiate it is situated dorsally on the hemisphere, in the border-region between pallium and subpallium. As the rostral prolongation is equally pronounced in these two parts, the olfactory bulb is always situated in the most rostral part of the hemisphere, a position which it retains in the adult animal.

The early ontogenetic development of the urodelan forebrain highly resembles that which we have found in Dipnoans, and the similarity to Epiceratodus is very conspicous. In fact, early ontogenetic stages of Urodeles resemble more closely the corresponding stages in Epiceratodus than the latter corresponds to Protopterus (cf. figs 1—3, 10—11, 15). In Urodeles there exist the same proliferation grooves and zones as in Dipnoi, and the two rostral zones give rise to the telencephalon. The hemispheric evagination starts as in Epiceratodus, and the lamina supraneuroporica partly evaginates to constitute a septum ependymale. From this develops as in Dipnoans a plexus choroideus lateralis and a plexus for the third ventricle, the latter, however, being in Urodeles an unpaired structure. In Dipnoi this plexus of the third ventricle is represented by infoldings from septum ependymale, dorsally to the foramen of Monroi (see p. 69). The structures characteristic of adult Urodeles and Dipnoans begin to be more noticeable rather late in the ontogenetic development.

ANURA.

Forebrain structures in adult Anurans are well known (for principal works see KAPPER, HUBER and CROSSBY 1936, p. 1491), while on the other hand the ontogenetic development of the same brainpart has, in comparison with the Urodeles been paid rather scant attention. GOETTE (1875) described the early ontogenetic development of the forebrain in Bombinator, and states that the primordium of the brain, in front of "die vordere Grenzfalte" (plica encephali ventralis), is divided into two parts which constitute a rostral and a caudal "Gewölbe". The ventricular boundary between these two is marked by "Sehnervenplatte" (terminal ridge). Dorsally this boundary is situated somewhat in front of the epiphysial opening. The rostral "Gewölbe" is "die gemeinsame Wurzel der beiden Gehirnlappen". GOETTE also points out that a basal part of the original rostral "Gewölbe" exists, which does not take part in the evagination. It remains at the chiasmatic ridge where it connects the two hemispheres. STUDNIČKA (1895) has investigated the development of the brain in Bufo, and is of the opinion that a great similarity exists between the

telencephalic development of this form and Petromyzon. He states that the first part of the telencephalon that begins to differentiate is the "Lobus posterior", and that later on there develops an "intercalare Portion der Hemisphäre" between this lobe and the olfactory bulb. The telencephalic part of the primitive forebrain is limited caudally by a "senkrecht verlaufende Rinne" (the sulcus intraencephalicus anterior of v. KUPFFER 1906). "Lobus posterior" is also bounded caudally by a fissure in the lateral prosencephalic wall. STUDNIČKA's posterior lobe corresponds to the pars post-foraminalis in adult brains of Amphibians and embryonic stages af lungfishes. v. KUPFFER has treated the ontogenetic development of telencephalon in Rana. He, however, does not add anything to the knowledge of the ventricular grooves and eminences. According to him there exists a "beachtenswerter Unterschied im Beginn der Hemisphärenbildung bei Urodelen und Batrachiern". In the first mentioned group, the hemispheres expand dorsally to begin with, in Rana and Bombinator on the other hand "richten sich die Hemisphären ... gleich anfänglich direkt frontalwärts ..." (p. 195). FUCHS (1908) has also investigated the conditions in Rana and she points out that a sulcus intraencephalicus anterior arises in connection with the development of the eye-vesicles. FUCHS is of the opinion that the cell-divisions, which cause the forming of the eye-vesicles, "auch im weiteren Umkreise bemerkbar machen und so, durch die Richtung des stärksten Wachstums hervorgebracht, jederseits eine furchenartige innere Erweiterung des Centralkanals ensteht". Sulcus intraencephalicus anterior thus develops in an area, the ventricular wall of which is the object of a rapid cell-proliferation. Ventrally this sulcus enters a part of this area where the proliferation is very pronounced, i.e. the optic evagination. FUCHS' observations are verified by my own investigations on Dipnoans and Urodeles, and we shall see that the same conditions also apply to the Anurans. According to FUCHS sulcus intraencephalicus anterior does not constitute a boundary between tel- and diencephalon, which v. KUPFFER thought. She considers it to be a diencephalic structure.

The only author who has made a more detailed investigation of the development of the Anuran telencephalon and its centers is SÖDERBERG (1922). According to her, grooves appear very early in the ventricular prosencephalic wall, which must be considered as boundary grooves of the primordia of the different telencephalic centers.

In order to investigate the nature of these grooves I have been studying early stages of Rana, Bufo, Pelobates fuscus and Xenopus laevis. The description, given below, is based on the conditions in Pelobates. The other Anurans, mentioned above, do not show any principal differences, and the telencephalic development in Pelobates may, therefore, be considered as a norm for the other species studied.

The ventral curving downwards of the primitive forebrain is very little

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pronounced. From the very beginning the floor of the prosencephalon (the floor of the future third ventricle) remains horizontal (fig. 17), and in later stages no curving upwards of the original prosencephalic part of the brain takes place. This is in contrast to the conditions in Dipnoans and Urodeles where this curving upwards is a very conspicous feature. In early ontogenetic stages the prosencephalon is divided into a rostral and a caudal part, which are separated from each other in the lateral wall by means of a sulcus di-telencephalicus (*s.d.t.*, fig. 17 A). This sulcus corresponds to the groove, which, according to STUDNIČKA, constitutes a caudal border to his "Lobus posterior". The two prosencephalic parts correspond to GOETTE's rostral and caudal "Gewölbe".

In the ventricular wall of the prosencephalon we have the same primary proliferation grooves as have already been described in Dipnoans and Urodeles, i.e. sulcus diencephalicus ventralis, sulcus intraencephalicus anterior and sulcus subpallialis (*s.d.v.*, *s.i.a.*, *s.sp.*, fig. 17 B—C). Between the first two there exists a di-telencephalic ridge (*d.t.r.*, fig. 17 B). This extends from the chiasma ridge (*ch.r.*, fig. 17 B) up to a point in the prosencephalic roof, just in front of the opening of the epiphysis (*ep.*, fig 17 B). GOETTE does not mention this ridge but he interprets the di-telencephalic boundary in early stages correctly. Somewhat in front of the epiphysis there exists a very inconspicous inward bulge in the roof (*v.t.*, fig. 17 B), which constitutes the rudiment of a velum transversum. In later stages this is situated immediately caudal to a slight evagination, which corresponds to a paraphysis (*par.*, fig. 17 E).

The sulci intraencephalicus anterior and subpallialis constitute together a crescent-shaped proliferation groove in the dorsal part of the telencephalic primordium (fig. 17 B). The hemispheric evagination starts with the appearance of a depression in the ventricular wall, just at the join of the two sulci, as was the case in Epiceratodus and Urodela. But in contrast to the conditions in these forms the rostral prolongation of the hemispheres starts without being preceded by a distinctly marked dorsally directed evagination (cf. figs 11—12, 15, 17). At the same time as the hemispheric evagination starts, the part of the lamina supraneuroporica, situated just in front of the paraphysial rudiment, begins to invaginate into the prosencephalic ventricle (*pl.ch.v.*, fig. 17 E). This invagination constitutes the rudiment of a plexus choroideus ventralis. During the subsequent development it increases in size, and more and more of the frontal prosencephalic wall becomes invaginated. This results in the obliterating of the paraphysis and the velum transversum, which are absorbed into the plexus ventralis (cf. fig. 17 E, I). That this structure really corresponds to the plexus choroideus ventralis of Urodeles (HERRICK 1934) is evident from the fact that it originates from the part of frontal wall situated in front of the rudimentary velum (*v.t.*, *pl.ch.v.*, fig. 17 E). Thus the lamina supraneuroporica does not contribute to any structures in the

medial hemispheric wall. In Anurans, therefore, we have no septum ependymale as in lungfishes and Urodeles.

In early stages of Rana, SÖDERBERG (1922) recognizes a pallium in the dorsal part of the telencephalic primordium. It is limited ventrally by a lateral sulcus E and a ventricular sulcus B, the latter being, according to SÖDERBERG, a sulcus limitans pallii lateralis. Sulcus B corresponds to a very conspicous groove, sulcus pallialis (*s.p.*, fig. 17 E—G), which according to my observations constitutes a proliferation groove in the dorsal part of the caudal telencephalic proliferation zone (pallial primordium). This part is characterized by having the ventricular cells arranged in distinct layers, one outside the other (fig. 17 K). The outermost layers show a tendency to detach themselves from the more ventricular layers. They represent the primordial cortex (*pall.c.*, fig. 17 K), which, as SÖDERBERG has shown, exists in embryonic stages of Amphibians. Sulcus pallialis is situated dorsally to the most ventral part of the pallial primordium (*s.p.*, fig. 17 K) and does not in early stages constitute a ventricular boundary of this primordium. This is evident from fig. 17 K. In the subsequent development, however, it shifts ventrally, and, in the adult brain, it constitutes a ventricular boundary groove to pallium, i.e. sulcus limitans pallii lateralis.

SÖDERBERG states that the external pallial boundary groove, sulcus E, is homologous to the fissura endorhinalis externa of reptiles "which in the latter forms an outer boundary groove for the pallial parts. In tadpoles as in reptiles, this groove frequently is continued by a set of blood-vessels which force themselves into the telencephalon in a position corresponding to that held by the groove" (p. 98). Of all the anurans investigated by me I have found SÖDERBERG's sulcus E only in Rana and Bufo. The groove, however, does not constitute an "outer boundary groove" as it is situated in the middle of the external surface of the pallial primordium, opposite to the sulcus pallialis, that is SÖDERBERG's sulcus B. In Bufo I have observed sulcus E in one specimen. It is, however, very short, and has been caused by a very conspicous blood-vessel, which penetrates the hemispheric surface at a place corresponding to the position of sulcus E in Rana. I have found that blood-vessels frequently enter the dorso-lateral parts of the hemispheric primordium, but in Anurans other than Rana I have not been able to determine any regularity in the appearance of these vessels, which ought to have caused the formation of a sulcus E. Sulcus pallialis (sulcus B), on the other hand, is a constant feature in all the anuran specimens investigated by me. Since sulcus E is not a permanent feature in Anurans, I do not feel inclined to consider it a boundary groove of the pallial formation, especially as, when it appears (Rana), it is situated within the pallial primordium.

The ventral part of the caudal telencephalic proliferation zone as in Dipnoans and Urodeles gives rise to the preoptic nucleus. With regard to the ventricular

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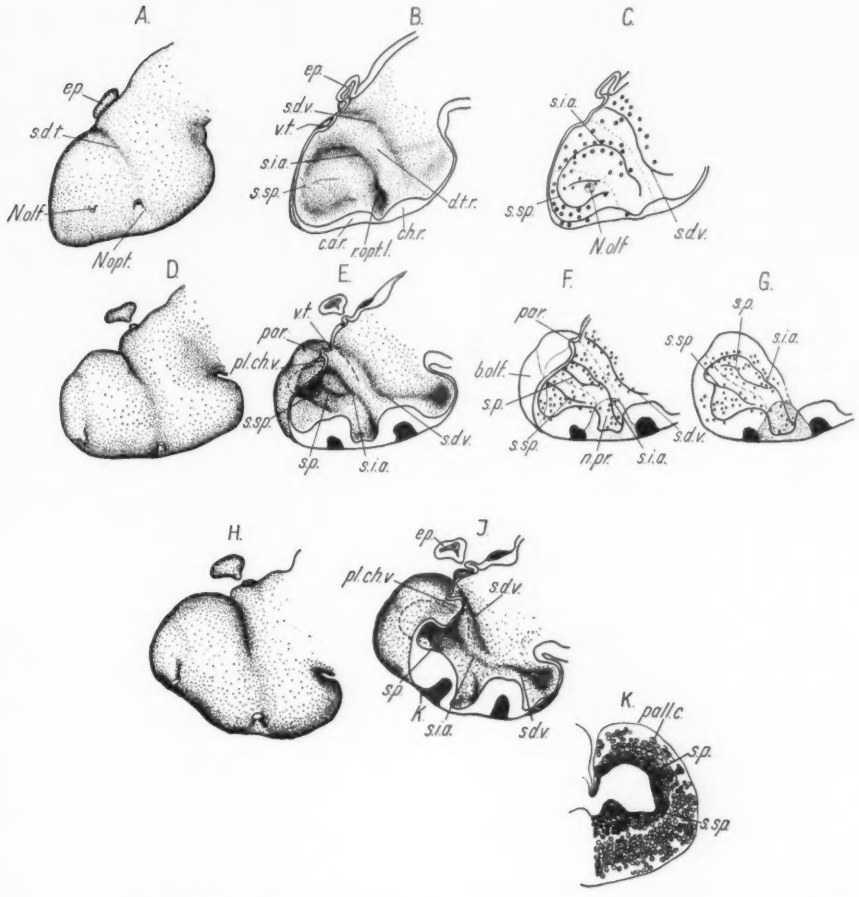

Fig. 17 A—K. *Pelobates fuscus.* Forebrain in 6 mm stage (A—C); 8 mm (D—G) and 8 mm, older stage (H—K). A—H graph.rec., 44x; K transv. sect. indicated in I by the letter K, 48x.

grooves situated in this part of the embryonic brain there is a difference between the Anurans and the other groups. Sulcus preopticus is not exactly homologous to the same groove in Dipnoans and Urodeles. In these it appears as an anterior, ventrally directed, branch of the intraencephalic sulcus, which in the later development becomes an independent groove in the ventricular wall of the preoptic nucleus. In Anurans the sulcus in question constitutes the ventral part of sulcus intraencephalicus anterior (*s.i.a.*, fig. 17 E), which separates from the more dorsal parts. These on the other hand seem to become joined to the ventral part of the sulcus diencephalicus ventralis (cf. fig. 17 E, I), and in this way give rise to the sulcus diencephalicus ventralis of older stages and the adult brain (*s.i.a.*, *s.d.v.*, fig. 17 I).

The subpallial proliferation zone differentiates around the sulcus subpallialis and is very soon easily distinguishable from the pallial primordium. No typical layers exist outside the ependymal cells as in pallium. Instead, the cells are arranged irregularily and separated distinctly from the ependymal layer by a cell-free zone (fig. 17 K).

In early stages the olfactory nerve enters the brain in the subpallial zone (*N.olf.*, fig. 17 A, C), and later on its entrance moves anteriorly, and in older stages, as in Urodeles, the primordium of the olfactory bulb occupies the most rostral part of the hemispheres (*b.olf.*, fig. 17 E, H).

In the Anurans we have the same proliferation zones and grooves as in Dipnoans and Urodeles, with the exception of the preoptic sulcus, which in Anura develops from the ventral part of the sulcus intraencephalicus anterior, not as an anterior branch of the same sulcus.

Rather early on, in the ontogenetic development several structures in the anuran forebrain differ from those met with in lungfishes and Urodeles. The ventral curving downwards of the prosencephalon is very inconspicous. The rostral prolongation of the hemispheres starts almost immediately without being preceded by a dorsally directed evagination (a fact already pointed out by v. KUPFFER). The pallial and subpallial primordia are easily distinguishable from each other very early in the ontogenetic development, a fact due to the different cellular arrangement in these two parts. Lamina supraneuroporica does not constitute a septum ependymale in the medial hemispheric wall. It is invaginated into the prosencephalic ventricle to form a plexus choroideus ventralis of diencephalon. As a result of this process the paraphysis and velum transversum are obliterated in marked contrast to the powerful development of these structures in Dipnoans and Urodeles.

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GROVES AND ZONES OF PROLIFERATION.

BERGQUIST's (1932) investigation shows that the grooves which appear in the ventricular wall of the diencephalon in early ontogenetic stages, do not constitute boundary grooves of the primordia of the different diencephalic centers. They are located inside certain areas of the ventricular wall, which are characterized by a very pronounced cell-proliferation, "Grundgebiete". The different centers develop later on from these areas, and in connection with this some of the proliferation grooves move from their original position and become boundary grooves, which in older embryonic stages and in the adult brain define the extent of these centers.

As is evident from the ontogenetical development of the forebrain of Dipnoans, Urodeles and Anurans, the same conditions exist in the telencephalon of these animals. In the early ontogenetical stages we always find in the

anterior part of the prosencephalon three, transverse proliferation grooves, i.e. sulcus diencephalicus ventralis, sulcus intraencephalicus anterior and sulcus subpallialis.

Sulcus diencephalicus ventralis.

According to BERGQUIST this groove constitutes a poliferation groove for the frontal parts of the diencephalon. It is well marked ventrally and here constitutes a proliferation groove of the hypothalamus. As is evident from a study of adult brains and older ontogenetic stages of Dipnoans and Amphibians, an unbrooken groove extends from foramen Monroi down into hypothalamus, the author's sulcus diencephalicus ventralis, which, however, does not correspond along its entire length to the embryonic proliferation groove sulcus diencephalicus ventralis. The rostral parts of the adult sulcus represent a remnant of the intraencephalic sulcus: which has, by means of a caudally directed growth, been connected to the ventral part of the embryonic ventral diencephalic sulcus. As a result of this the ventral diencephalic sulcus and its most ventral component, the hypothalamic sulcus, extends in the adult animal between the foramen Monroi and the infundibulum.[1]

Sulcus intraencephalicus anterior.

This is the caudal one of the two grooves of proliferation which are located in the telencephalic primordium. It always extends between recessus opticus lateralis and a point just in front of the velum transversum. The hemispheric evagination starts by a deepening of the dorsal part of this sulcus. Its ventral part, as has already been stated, loses its connection with the lateral optic recess and becomes connected with the sulcus diencephalicus ventralis. By this process this part of the groove no longer constitutes a proliferation groove. Instead, it becomes a dorsal ventricular boundary groove of the preoptic nucleus.

As has already been mentioned, STUDNIČKA has observed the sulcus intraencephalicus anterior, and is of the opinion that it constitutes a boundary groove between diencephalic and telencephalic primordia in the primitive forebrain. KUPFFER has given the groove its name and in investigating different lower vertebrates he finds this groove "ausgeprägt bei allen Ichtyopsiden. Sie bildet wie die hintere eine wichtige Grenzmarke zwischen zwei Regionen des Vorderhirnes" (p. 47). "Das Telencephalon erhält stets durch den Sulcus intraencephalicus anterior und das Velum transversum seine natürliche hintere Begrenzung" (p. 136). HERRICK finds in Amblystoma a ventral, diencephalic

[1] According to KUHLENBECK (1929b) and HALLER (1929) sulcus hypothalamicus only seemingly constitutes a continuation of the sulcus diencephalicus ventralis. In all Dipnoans and Amphibians investigated by me I have found these two grooves to constitute an unbroken groove from the foramen Monroi down into the infundibulum.

groove, sulcus diencephalicus ventralis, "Immediately behind the commissural ridge in Amblystoma the ventral sulcus divides. One part follows the caudal border of the ridge into the preoptic recess. This is the ventral part of KUPFFER's sulcus intraencephalicus anterior. The other part continues caudad dorsal to the preoptic nucleus and chiasma ridge to terminate blindly in the caudal part of the hypothalamus. It marks the boundary between the preoptic nucleus and hypothalamus and the thalamus in front..." (HERRICK 1910; p. 419). The part of the intraencephalic sulcus, which according to HERRICK extends down into the preoptic recess, is the same as my sulcus preopticus. The other branch corresponds to the part which, in Dipnoans and Urodeles, forms a part of the sulcus diencephalicus ventralis of the adult animal. This is evident from the ontogenetic development.

HERRICK (1917) states concerning the conditions in the adult Necturus, "The hypothalamus and chiasma ridge are separated from the preoptic nucleus by an oblique ventricular sulcus which runs foreward and ventralward in front of the chiasma ridge to end in the deep preoptic recess (figs 63, 64). This I interpret as a persistent portion of the anterior end of the embryonic sulcus limitans". If a sulcus limitans existed in this parts of the primitive forebrain it should cross the sulcus diencephalicus ventralis and the ditelencephalic ridge, but I have not been able to find any evidence of this condition in all the embryonic stages of Amphibians and Dipnoans investigated by me. The works of KINGSBURY (1920, 1922) and JOHNSTON (1923) show that sulcus limitans can at most be traced to the recessus mamillaris.[1] The powerful development of the commissural ridges on each side of the compressed preoptic recess in lungfishes and Amphibians, causes these ridges to bulge somewhat into the recess. By this means there arises a fold between the ridges and the ventricular wall of the nucleus preopticus. The position of the groove, which according to HERRICK constitutes the anterior part of sulcus limitans (see his fig. 63), argues in favour of there being such a fold between the ventricular wall and the chiasma ridge.

In a later Amblystoma-paper (1927), HERRICK points out that "Behind the anterior commissure ridge the sulcus intraencephalicus anterior (figs 1, 12, *s.ie.ant.*) of von Kupffer ('06, p. 175, fig. 187) separates the bed nuclei of the commissure from the nucleus preopticus" (p. 238), and the same holds true for Necturus (1933 a). HERRICK finds that according to the investigations of BAKER and GRAVES (1932) on Amblystoma jeffersonianum "it is evident that the sulcus preopticus (their s. ventroventralis) is from its first appearance directly continous with von Kupffers sulcus... I have previously illustrated ('24 a fig. 6) a model of a 30 mm larva of A. jeffersonianum in which the sulcus intraencephalicus anterior enters in a depressed area as in larval Nec-

[1] See also LEHMANN (1941).

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turus and there divides into anterior and posterior branches, i.e. into s.ie.ant. and s.po." (HERRICK 1933 a; p. 242).

As is evident from the ontogenetic development in lungfishes and Urodeles, it is the anterior branch which constitutes a sulcus preopticus, not the posterior, which fuses with the sulcus diencephalicus ventralis. In the adult brain there appears only one sulcus in the ventricular wall of the nucleus preopticus, sulcus preopticus. HERRICK, however, also finds a groove immediately dorsal and caudal to the ridge of the anterior commissure. He consideres this groove to be the anterior branch of the intraencephalic sulcus. The ontogenetic development of lungfishes and Urodeles, however, has shown that this groove is a caudal continuation of the embryonic sulcus subpallialis, dorsally to the ridge. This part of the sulcus is continued ventrally, immediately behind the ridge, by a fold in the ventricular wall, caused in the same manner as that immediately anterior to the chiasma ridge (see above). This also seems to be case in Amblystoma, judging from the figures in the 1927-paper of HERRICK. On his fig. 1 a groove, *s.ie.ant.* exists, which follows the dorsal and caudal parts of the anterior commissure ridge. Its position corresponds exactly to the caudal continuation of the sulcus subpallialis in Dipnoans and Urodeles.

According to the earlier authors (cf. v. KUPFFER 1906), the primitive forebrain is divided into three vesicles, which are separated by ridges. HALLER (1929) discussed these conditions, and considered that the first ventricle ("Leistung") develops into telencephalon. The second gives rise to a groove, sulcus medius, which constitutes a boundary between a caudal and a rostral part of thalamus. This latter part develops from the ridge ("Leist") between the first and the second vesicle. HALLER states that the ventral part of this ridge is divided by the sulcus intraencephalicus anterior, which sends out a branch on each side of the velum transversum. I have never been able to observe such a course for the groove in question. HALLER's embryonic investigations have been made on Acanthias, but BERGQUIST's on the same form, which I have been able to verify, do not show a dorsally directed branching of the intraencephalic sulcus, with the velum transversum situated between these branches. The ridge which separates the first and second vesicles, extends, according to HALLER, between the chiasma ridge and the velum transversum, and thus corresponds to my di-telencephalic ridge. HALLER's sulcus medius corresponds to my sulcus diencephalicus ventralis.

HALLER is also of the opinion that sulcus limitans of HIS is representated in adult Rana by an anterior, ventrally directed branch of the sulcus diencephalicus ventralis. The ontogenetic development of Anurans shows that this "branch" is the ventral part of the embryonic intraencephalic sulcus, which in the adult animals constitutes a sulcus preopticus.

Sulcus subpallialis.

This groove is the foremost of the three proliferation grooves in the anterior part of the primitive forebrain. In early embryonic stages the dorsal parts of this groove become connected with the dorsal parts of sulcus intraencephalicus anterior, and the hemispheric evagination starts at the join of these two grooves. In the forms investigated by me the subpallial sulcus behaves somewhat differently during the development. In Protopterus it constitutes a proliferation groove of the subpallial parts of the telencephalon. When the hemispheres begin to expand the dorsal parts of the subpallial sulcus, forms the anterior boundary groove of the lateral ventricle. As a result of the increasing evagination, the ventral parts of the groove are also drawn into the hemispheric primordium, and, in older stages and in the adult animal, the groove joins the ventral corner of the hemispheric ventricle. The most ventral part, however, is left in telencephalon medium, where it constitutes a lateral boundary groove to the nucleus of the anterior commissure.

In Epiceratodus the same conditions exist to begin with. In older stages the sulcus does not descend to become the angulus ventralis. It remains in the ventricular wall of the hemisphere, where it constitutes a boundary groove between nucleus olfactorius lateralis and the tuberculum olfactorium, sulcus limitans lateralis (HOLMGREN 1922). In somewhat older stages and in the adult brain it has been obliterated.

In Necturus we find the same conditions as in Epiceratodus, i.e. sulcus subpallialis starts as a proliferation groove and in later stages becomes a boundary groove between nucleus olfactorius lateralis and tuberculum olfactorium.

In Anurans the sulcus constitutes the angulus ventralis of the lateral ventricle, analogous to the conditions in Protopterus.

The only auther who mentions any grooves anterior to the intraencephalic sulcus in the embryonic forebrain is SÖDERBERG, who has observed some grooves in the telencephalic primordium of Rana. According to her there exists in this animal a sulcus C, which becomes the "floor groove" of the lateral ventricle, and in early stages this groove is situated well up in the ventricular wall in the part of the telencephalic primordium which have not as yet been evaginated. A comparison between my figs 17 B, E, I and SÖDERBERG's figs 3 and 7 shows that her sulcus C is homologous to my sulcus subpallialis. In Triton sulcus C is situated in the ventricular wall and, according to SÖDERBERG, constitutes in older embryos a groove "dividing striatum from the septum portion of the forebrain". My own investigations of Triturus (Triton) and Hynobius show that the subpallial sulcus in these animals is more or less obliterated during the development, and that it is impossible to decide whether the

grooves, which appear in older embryos in the ventral parts of the lateral wall of the hemispheric ventricle, have developed from the embryonic subpallial proliferation groove or not.

Sulcus pallialis and sulcus subpallialis dorsalis.

BERGQUIST points out that the diencephalic proliferation grooves often vary in their position and that they "bei verschiedenen Tiere oft nicht als stricte homolog angesehen werden können" (p. 73). This statement is not true of the two primary telencephalic proliferation grooves, sulcus subpallialis and sulcus intraencephalicus anterior, as I have always found them in the same position and relation to each other as long as they constitute proliferation grooves. During the development other grooves appear which do not, however, exist in all the species investigated. For a longer or shorter period, they constitute proliferation grooves in the pallial and subpallial primordia. In Protopterus there exists in the pallial part of the embryonic hemisphere a sulcus pallialis, which during the development moves down ventrally, and which in older embryonic stages constitutes a ventral boundary groove to the pallium, the sulcus limitans pallii lateralis of the adult brain. The foremost parts of this sulcus seem to have been built up of a dorsal, subpallial proliferation groove, the sulcus subpallialis dorsalis, which has shifted dorsally. This groove is, to begin with, a proliferation groove of nucleus olfactorius lateralis. In Anurans the sulcus pallialis is very conspicous (sulcus B in Rana according to SÖDERBERG), and as in Protopterus it becomes the sulcus limitans pallii lateralis of the adult anuran forebrain. In Urodeles I have not seen anything corresponding to the sulcus pallialis. In Epiceratodus a sulcus appears in later embryonic stages in one specimen which may be a sulcus pallialis, but it is very soon obliterated.

In early embryonic stages of Rana there appears a subpallial groove (sulcus G according to SÖDERBERG), and I have found this groove in some of my specimens of Bufo, Pelobates and Xenopus. This sulcus constitutes a proliferation groove in the dorsal part of the subpallial proliferation zone, i.e. the primordium of the lateral olfactory nucleus, and thus corresponds to the sulcus subpallialis dorsalis of Protopterus. Contrary to the conditions in this animal, it descends ventrally and becomes a ventral boundary groove to nucleus olfactorius lateralis, i.e. it is a sulcus limitans lateralis. This groove thus develops in Anurans from a quite different proliferation groove than in Epiceratodus and certain Urodeles (Necturus). In these forms the groove in question develops from the sulcus subpallialis. In Protopterus no sulcus limitans lateralis exists.

In Dipnoans and Amphibians, a short proliferation groove sometimes appears inside the primordium of the olfactory bulb, but it does not give rise to a boundary groove.

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The following table shows the different proliferation grooves in the telencephalic part of the primitive forebrain and their derivatives in the adult brain.

S.int.ant.	proliferation groove of pallium and nucl. preopt.; Dipnoans, Amph. . .	*anter.part of s.dienc.v.;* Dipn.Amph. *s. preopt.,* Anura.
S.subpall.	proliferation groove of subpall; Dipnoans, Amphibians	*ang.ventr.;* Protopterus, Anura; *s.lim. lat.;* Epiceratodus, Necturus.
S.preopt.	proliferation groove of nucl. preopt.; Dipnoans, Urodela	*sulc.preopt.;* Dipnoans, Urodela.
S.pall.	proliferation groove of pallium; Protopterus, Anura	*sulc.lim.pallii lat.;* Protopterus, Anura.
S.subp.dors.	proliferation groove of nucl. olf. lat; Protopterus, Anura	*sulc.lim.pallii lat.;*Protopterus; *sulc. lim. lat.;* Anura.

Proliferation zones.

Around the above mentioned proliferation grooves we have three proliferation zones which constitute primordia of di- and telencephalic centres. The anterior telencephalic zone gives rise to subpallial structures, i.e. nucleus olfactorius lateralis, tuberculum olfactorium and the septal formations. Pallium develops dorsally from the posterior zone, and nucleus preopticus ventrally.

In a number of papers (i.e., 1928—1930) COGHILL has shown that as a result of the position of the neuroblasts, it is possible to distinguish 16 areas in front of the isthmus in early embryonic stages of Amblystoma. HERRICK (1937, 1938) has investigated these areas and their future development, and has drawn some reconstructions of the brain of embryonic stages of Amblystoma in which he has marked the extent of COGHILL's areas. HERRICK states that "The adult equivalents in some cases are clear, in others they are uncertain pending further study of intervening stages and internal structure. Few of the boundaries which are delimited on these figures are sharply defined and their interpretation is based in part on study of relations in older larvae" (p. 392; 1937).

In fig. 18 A I have superimposed on HERRICK's fig. 16 (1938 a) the extension of the telencephalic proliferation zones found during my observations on Urodeles. In figs 16 and 18 (my figs 18 A, B) HERRICK (1938 a) has drawn two grooves in the anterior part of the prosencephalon. The rostral one, not described by HERRICK, is sulcus subpallialis (*s.sp.*, fig. 18). The caudal groove is the sulcus intraencephalicus anterior (*s.i.a.*, fig. 18). From fig. 18 A it is evident that the subpallial proliferation zone around sulcus subpallialis includes the areas 1, 4 and 4 a of COGHILL. In 1937 HERRICK defined these areas and he states that 1 is an "area olfactoria primitiva" and that it receives "Coghill's nervus terminalis and subsequently the definitive olfactory nerve. It is certainly the primordium of the olfactory bulb and probably of some adjoining parts

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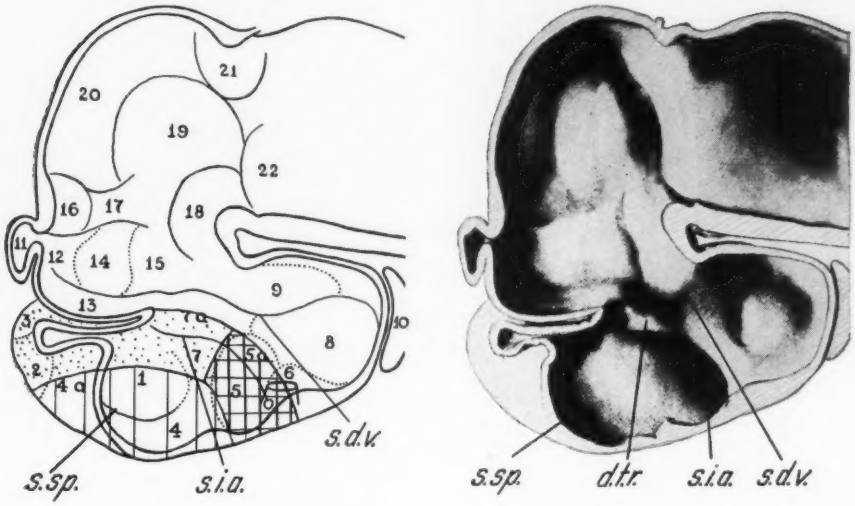

A. B.

Fig. 18 A—B. *Amblystoma tigrinum*. Brain in younger larva (after HERRICK 1938 a). In A I have indicated the position of the subpallial (vertical lines) and pallial (dotted) zones together with the primordium of the preoptic nucleus (cross-hatched).

(e.g. nucleus olfactorius anterior)" (p. 392). Area 4 constitutes a primordium of the septum, the dorsal parts of which (4 a) "probably forms the rostral end of the lateral olfactory nucleus, including the area which I have regarded as primordium of the head of the caudate nucleus ('27, p. 296)". Areas 1, 4 and 4 a are all developed out of my subpallial proliferation zone, and the position of the entrance of the olfactory nerve is the same as I have found in Dipnoans and Amphibians, i.e. in this zone and distinctly separated from the first evaginated part of the hemispheric primordium.

The caudal telencephalic proliferation zone around sulcus intraencephalicus anterior, includes the areas 2, 3, 5, 5 a, 7 and 7 a. According to HERRICK 2 constitutes a "primordium piriforme" and 3 a "primordium hippocampi". 5 and 5 a are the primordium of the preoptic nucleus (pars inferior). 7 is the "strioamygdaloid area". 7 a is an area the future fate of which is rather uncertain, "in later stages it seems to be incorporated into the ventral thalamus". In Protopterus, the parts corresponding to area 7 and 7 a give rise to the pars superior of the preoptic nucleus, and probably also to the nucleus ventralis thalami, which becomes closely connected with pars superior (see p. 117).

Naturally it is impossible to define the exact boundaries of the proliferation zones from the position of the mitoses only. Their extension varyes from stage to stage and from specimen to specimen in the same stage of development. My own investigation as compared with those of HERRICK, however, seems

to indicate that around the sulcus intraencephalicus anterior we have an area which in its dorsal parts gives rise to the pallial formation, both in Dipnoans and Amphibians (areas 2 and 3 of HERRICK—COGHILL). From the ventral part of the area in question develops a pars inferior (5 and 5a) of the preoptic nucleus. Between these two primordia there develops in Protopterus a pars superior of the same nucleus, which possibly corresponds to the "strioamygdaloid complex" of the Amphibia (see p. 130).

HERRICK (1933d) refers to BERGQUIST's investigation and points out that "before elaborating a general morphological schema on these centres of proliferation alone it would seem expedient to inquire farther into their causes and relations with other morphogenic agencies" (p. 244). Among these agencies Herrick mentiones the differentiation of cellular elements and refering to COGHILL's papers (i.a., VIII, 1928) he points out that "the differentiation of indifferent cells into neuroblasts is accelerated in the areas between the centers of active proliferation and in later stages this is between the sulci" (pp. 244—245). He further states that the non-specific area of proliferation and the specific area of differentiation are both "morphogenic agencies which act at different times and in different places ..... But for practical purposes of descriptive anatomy and experimental physiology the differentiation, which looks forward to functional efficiency, is vastly more significant;...." (p. 245).

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It seems to me, judging from my own investigations, that the differentiation, at least in telencephalon, does not start between the primitive proliferation zones but inside these. It is evident from the ontogenetic development that the pallium differentiates inside the dorsal part of the caudal telencephalic proliferation zone, around the angulus dorsalis of the lateral ventricle, which is an extension of the old proliferation groove sulcus intraencephalicus anterior. Several centres differentiate inside the subpallial zone. In the lateral wall we have for instance the primordia of nucleus olfactorius lateralis and tuberculum olfactorium. There often appear secondary proliferation grooves inside these centres. It is true that in "later stages" the areas of differentiation are situated between the sulci, but the ontogenetic development shows that some of the proliferation grooves move from their original position inside the proliferation zones to become boundary groves for areas of differentiation, and that these movements take place at the time when the centres of differentiation begin to be distinguishable.

In the adult forebrain the telencephalic centers extend horizontally, and the subpallium is situated ventrally in relation to the pallium. BERGQUIST is of the opinion that the proliferation zones originally extend dorso-ventrally (transversally). "Ich meinerseits schliesse mich ziemlich vorbehaltslos der von Schilling, Röthig, Haller u.a. vertretenen Auffassung von einer morphologisch vertikalen Zellenverteilung im oberen Thalamus an. Die Berechtigung dieser

Auffassung dürfte auch bereits so deutlich aus dem Stadienbeschreibung, die oben für verschiedene Tiere geliefert worden sind, hervorgegangen sein ....." (p 252).

The ontogenetic development shows that the proliferation grooves and zones extend vertically between the roof and the floor of the primitive forebrain. In fig. 19 I have tried to show diagramatically the position of these structures as they appear in the ventricular wall of the prosencephalon during different ontogenetic stages. The conditions in telencephalon are based on my own observations on Dipnoans and Amphibians. For diencephalon I have used BERGQUIST's results. From fig. 19 it is evident that the ventral curving downwards of the primitive forebrain causes the originally transversal grooves and zones to become apparently horizontal. During the subsequent development the telencephalic primordium is bent up dorsally and in this way the structures in question again become more less vertical. Finally the rostral prolongation sets in and causes the horizontal extension of the telencephalic centres in the adult animal.

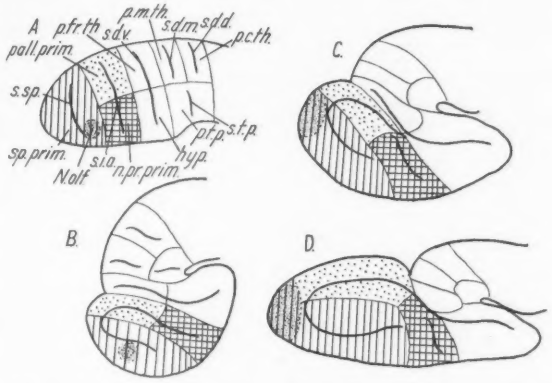

Fig. 19. Schematic drawing of the arrangement and the development of the procencephalic proliferation grooves and zones in an amphibian or lungfish.

In the development sketched above, variations exist in the different groups investigated. The Anurans especially differ in having a very inconspicous ventral curving downwards of the prosencephalon, and the telencephalic areas in this group have, therefore, a more vertical position during a greater part of the development. HALLER (1922) states that there does not exists any difference in the ventral curving downwards of the primitive forebrain in Anura and Urodela. "Im Hinblick auf die Hirnbeugen gehört das Gehirn den Amphibien zum Typus der Knochenfische und Ganoiden. Die Dottermasse, die der Embryo fest anheftet, verhindert dort eine ausgiebige Beugung des vorderen Hirnschenkels. In Zustand der grössten Hirnbeuge schliesst die Zwischenhirnachse mit der Achse des Myelencephalons einer Winkel von 90° ein. In dieser Hinsicht verhalten sich die Urodelen und Anuren gleich" (p. 170). As measure of the downward curvature (Kopfbeuge) HALLER indicates the angle between two axes, one the axis of the myelencephalon and the other passing through the terminal ridge and the midpoint between the position of the posterior commissure and the tuberculum posterior. In fig. 20 I have

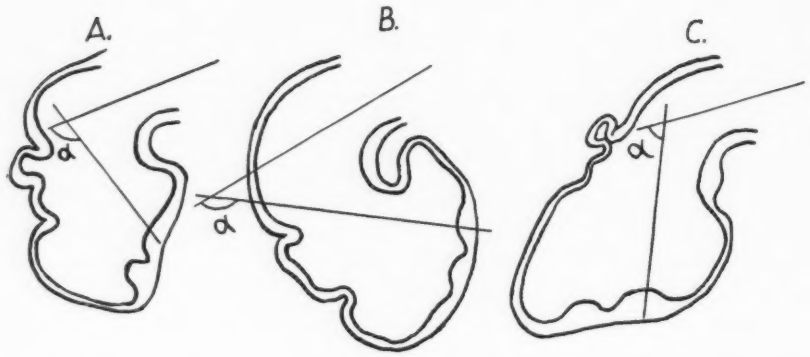

Fig. 20. The outline of prosencephalon in early stages of *Epiceratodus* (A), *Triturus* (B) and *Pelobates* (C).

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indicated the outlines of the prosencephalon in Epiceratodus, Necturus and Pelobates in a stage when the ventral curving downwards is most conspicous, and drawn the axes mentioned by HALLER. From the figure it is evident that in Dipnoans and Urodeles the angle (α) which marks the "Kopfbeuge" is much greater than in the Anurans.

These differences, however, do not have any influence upon the fact that the primordia of the telencephalic and diencephalic centers extend from the floor to the roof in the ventricular wall of the primitive forebrain. JOHNSTON (1911 b) has pointed out that "The antagonism between the apparent morphological plan of the amphibian brain and the fundamental morphological plan of the vertebrate brain set forth by His arises from the fact that the amphibian telencephalon is secondarily greatly elongated. The same divisions are seen in the selachian brain but do not suggest longitudinal columns. They are rather transverse divisions and the line separating them ends in the roof" (p. 540).

The hemispheric evagination.

According to GOETTE (1875) the lateral walls of the primitive forebrain on each side of the thin roof turn outwards to form the primordium of the hemispheres, "welche gerade vorwärts und gegen das Ende verjüngt sich hinziehen, dagegen rückwärts in zwei viel kleinere, divergierende und der hintere Gewölbe überragende Ecken auslaufen". STUDNIČKA (1895) states that the polus posterior, the "divergierende Ecken" of Goette, is the first part of the hemisphere to appear. HERRICK (1921 a) is of the same opinion. According to him the hemispheric evagination does not start in the part of the primitive brain containing the bulb, but instead begins "at the extreme caudal end of the endbrain just in front of the velum transversum. This region which forms

the posterior pole of the hemisphere is well evaginated before there is any notable outpoaching in the rostral part of this endbrain close to the lamina terminalis which lies adjacent to the nasal sac and which will later form the olfactory bulb" (p. 443). According to HERRICK this also holds true for lungfishes, but the conditions there are complicated as "the olfactory bulb develops not at the rostral end of the primitive endbrain, but on the dorsal border near its caudal end in immediate contact with the nasal sac" (p. 443).

SÖDERBERG (1922) on the contrary states, "It is true that in a reconstruction of the brain of such an embryo an evaginated part is visible, and has been interpreted as a caudal lobe. This is, however, the anterior part of the telencephalon as is clearly evident from, inter alia, the position of the rudiment of the bulbus olfactorius. The roof of the forebrain therefore already occupies its normal position, and the continued increase in growth of the brain does not cause the now ventral part to turn upwards as would be the case if the already evaginated portions where the caudal lobes" (p. 110).

BURR (1922) points out that the dorsal (anterior according to BURR) third of sulcus intraencephalicus anterior "is more deeply marked than in the posterior two-thirds and represents the site of the future evagination of the hemisphere" (p. 285). Further he states that the first evaginated parts "bears no apparent relation to the nasal placode, since it occurs dorsally and anteriorly to it" (p. 286).

BAKER and GRAVES (1932) are of the same opinion as HERRICK concerning the parts to evaginate first. "From a critical study of material, showing the primordia of the cerebral hemispheres, it may be infered that the beginning evagination of the lateral ventricle of the previous Stage 3 (10 mm) marks the position of the posterior horn of the ventricle of the present brain ....." (p. 514).

The ontogenetic development in Dipnoans shows that the hemispheric evagination starts immediately in front of the velum transversum, that is in the dorsal parts of the pallial proliferation zone. At this time the entrance of the olfactory nerve is situated in the ventral parts of the subpallial zone, distinctly removed from the first evaginated parts of the hemispheres. As a result of the increasing evagination the subpallial parts are drawn into the hemispheric primordium. At the same time the entrance of the olfactory nerve is pushed upwards in dorsal direction and when the olfactory bulb begins to differentiate it is situated immediately in front of the pallial parts of the hemisphere, i.e. the part which began to evaginate first. This part begins to extend rostrally very late in the development, and together with the olfactory bulb partakes in the formation of the rostral parts of the hemispheres.

In Amphibians the hemispheric evagination starts in the same manner, that is in the pallial primordium immediately in front of the velum, and here also

we find the entrance of the olfactory nerve in the subpallial proliferation zone. During the development the entrance of this nerve is pushed in an anterior direction, but unlike the conditions in Dipnoans, when the bulb begins to differentiate it is situated in the most anterior part of the hemisphere. This is due to the simultaneous rostral prolongation of the pallial and subpallial parts.

The caudal lobe (posterior pole of HERRICK, 1921 a) in the amphibian brain, and which in the adult forebrain constitutes a very conspicous feature, contains exclusively pallial elements and has thus d e v e l o p e d out of the parts first evaginated. But as this structure appears relatively late in the development it does not from the beginning c o n s t i t u t e the first evaginated part. The turning upwards of the first evaginated parts, which according to SÖDERBERG must exist if the caudal lobe has developed out of these parts, actually occurs as has already been pointed out (p. 24).

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THE DEVELOPMENT OF THE LATERAL CHOROIDAL PLEXA IN DIPNOI.

In the structure of the medial hemispheric wall there is a remarkable contrast between the two types of dipnoan forebrains. In Epiceratodus the dorsal part of this wall constitutes a powerfully folded epithelial membrane, which extends between the medial parts of the pallium (hippocampal formation) and pars dorsalis of the septum. That this choroidal membrane belongs to the medial hemispheric wall and does not constitute an unpaired rostral continuation of the supraneuroporic lamina (BING and BURCKHARDT, 1905), is clearly shown by HOLMGREN and VAN DER HORST. In Protopterus and Lepidosiren the medial parts of the pallium and the septum meet in the dorso-medial corner of the hemisphere, without any intervening membrane. There exists another difference as these two species both have a powerfully developed plexus choroideus lateralis, which almost fills up the entire lateral ventricle in the adult brain. According to HOLMGREN and VAN DER HORST this structure is restricted in Epiceratodus to a brush of choroidal folds in the vicinity of the foramen of Monroi.

A comparison between Stage 4 of Epiceratodus (fig. 13) and Stage 6 of Protopterus (fig. 7) does not show any such difference in the structure of the medial wall. This wall in both genera is built in the same way, with the exception of the somewhat greater extent of the septum ependymale in Epiceratodus, in which form it extends in front of the foramen Monroi, conditions which do not exist in Protopterus.

HOLMGREN and VAN DER HORST point out that the difference in structure existing in the medial hemispheric wall in dipneumonian and monopneumonian lungfishes depends on the fact that in early stages of Epiceratodus the hemi-

spheric evagination starts at the join of the epithelial wall, of the prosencephalic ventricle (lamina supraneuroporica, which is rather broad in this species), and the nervous lateral walls of the same brainpart. Thus the lateral parts of the supraneuroporic lamina become evaginated, and constitute the epithelial part of the medial wall in the hemispheric primordium (septum ependymale). In Lepidosiren, however, the lamina supraneuroporica is very narrow and the hemispheric evagination begins in the lateral walls, well removed from the lamina, which therefore does not become evaginated so that no epithelial part of the medial hemispheric wall exists in the adult brain of this form.

The ontogenetic development confirms HOLMGREN's and VAN DER HORST's conception concerning the origin of the epithelial part of the septal wall in Epiceratodus ("lingula interolfactoria", BING and BUCKHARDT). In order to draw a complete comparison with the conditions in Protopterus, however, we must investigate the development of the plexus choroideus of the lateral ventricle.

KERR (1902) states that the parts of the hemisphere which in embryonic stages border on to the thalamus, i.e. the caudal parts of the medial wall, are very thin and from these parts the lateral plexus develops in the form of an invagination into the lateral ventricle of the hemisphere. Similar conditions exists in Protopterus in Stage 5, where there is an inconspicous invagination in the caudal parts of the medial wall of the hemispheric ventricle (*pl.ch.l.*, figs 5 D; 6 B). These facts argue against HALLER's conception (1934), that in reptiles "finden wir zum ersten Mal die Anlage einer echten Lateralplexus, d.h. eine solchen, der von den Wandungen der Hemisphären seinen Ursprung nimmt".

According to ELLIOT SMITH (1908) the lateral plexa in Dipnoi and Mammalia originate from three different parts of the embryonic brain: a) they contain a derivative from the roof of the primitive forebrain, which has evaginated into the hemisphere, a conception which corresponds to that of HOLMGREN and VAN DER HORST, referred to above; b) they originate partly from a more caudally situated area, i.e. the border region between the pallium and the thalamus which "becomes stretched and attenuated .... to form the caudal part of the lamina choroidea" (KERR's conception regarding the development of the plexus lateralis in Lepidosiren); c) a third part the plexus choroideus receives from the dorsal, caudal part of the "paraterminal body" (pars dorsalis septi) which borders on to the hippocampal formation. The nervous elements become reduced, and the area in question obtains an epithelial structure. ELLIOT SMITH remarks that in Epiceratodus "the thinning of the dorsal part of the paraterminal body extends forward ..... for a considerable distance (even perhaps the greater part of the hemisphere), and when the invagination of the roof membrane begins (at the foramen of

Monroi) to form the choroid plexus, the process of folding extends forward in the attenuated portion of the paraterminal body" (p. 538).

In Protopterus the evagination starts dorsally in the dorsal parts of the prosencephalon, but not in immediate connection with the epithelial roof as in Epiceratodus but at some distance ventrally to this (fig. 1 B). The supraneuroporic lamina is very narrow and does not in any way extend to the part of the lateral wall, wich begins to evaginate first. During the early ontogenetic development the epithelial part of the medial wall (septum ependymale) starts as a thinning of this wall, and later on is restricted to its caudal parts. This area has developed laterally and ventrally to the supraneuroporic lamina and thus does not contain any parts of the epithelial roof of the prosencephalon.

During the later ontogenetic development the evaginated part of the lamina supraneuroporica in Epiceratodus (septum ependymale) begins to increase, and in Stage 4 it constitutes the greatest part of the medial ventricular hemispheric wall (*s.ep.*, fig. 13 D). In Stage 5 the area occupied by the septum ependymale seems to have been somewhat reduced, but lateral folds now begin to appear in it (*pl.ch.l.*, fig. 14 D, F). The anterior part of the medial hemispheric wall contains the septal formation (ELLIOT SMITH's paraterminal body).

After Stage 5, however, the septum ependymale increases again considerably in size in connection with the rostral prolongation of the pallial parts of the hemispheres. As the septum ependymale is attatched by its dorsal border to the medial pallial parts, it is carried away in this prolongation. Coincident with this is the ventrally directed extension of the subpallial parts, which further increases the elongation of the structure in question. At the same time, however, there must exist a rapid proliferation of cells in this lamina because the folds, which began to appear in Stage 5, increase very much in number and size in spite of the considerable elongation the ependymatic septal wall is exposed to. In the adult brain it has developed into the enormous, richly folded epithelial membrane (lingula interolfactoria) which constitutes the dorsal part of the medial wall of the hemisphere. Unfortunately, owing to the scantiness of my material of older developmental stages, I have not been able to follow these conditions very closely in Epiceratodus, and the description above concerning the development of septum ependymale after Stage 5 must, therefore, be more or less hypothetical. As far as I can see, however, there is no other way to explain this development unless we accept ELLIOT SMITH's conception that the powerful development of the ependymatic septal wall in later stages is due to a reduction of the nervous elements in the dorsal parts of the paraterminal body. But if such a reduction really existed, we ought to find some traces of it in Stage 5. I have, however, not been able to establish any such traces. The reverse conditions if anything exist, since the septum ependymale in this stage is somewhat compressed

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compared with Stage 4, as the pars dorsalis septi (paraterminal body) begins to develop. The latter structure, judging from the conditions in the adult brain, must have undergone a development no less than that of the epithelial part of the septal wall, conditions which do not speak in favour of a reduction.

In Protopterus conditions are quite different. In Stage 5 the septum ependymale occupies a relatively great deal of space, but in the subsequent development pars dorsalis of the septum increases very rapidly and the septum ependymale becomes compressed and pushed into the lateral ventricle in a single fold, which begins to appear as early as in Stage 5. As a result of a rapid cell-proliferation in this fold it increases very much, and in the adult brain it constitutes the great plexus choroideus of the lateral ventricle. From a comparison of the medial walls in Stage 5 of Protopterus (fig. 5 D) and Stage 4 of Epiceratodus (fig. 13 D) it is evident that extensive contact exists between the nervous septal parts and the pallium in Protopterus. In Epiceratodus, on the other hand, the septum ependymale separates these telencephalic centers from each other, and these conditions seem to explain the fact that in Epiceratodus the septum ependymale follows the rostral pallial prolongation, while this process in Protopterus is prevented by the part of pars dorsalis septi which borders on to the pallium.

From the ontogenetic development of the lateral folds of the septum ependymale it is evident that the great number of folds in the dorsal part of the septal wall in Epiceratodus corresponds to the single fold in Protopterus, i.e. constitute a lateral choroidal plexus.

In the adult brain of Protopterus the septum ependymale persists as a small ependymatic area dorsal to the foramen Monroi, and from it some short folds hangs down in the anterior part of the third ventricle, caudally to the plexus choroideus lateralis and laterally to the velum transversum (*pl.ch.III.*, fig. 29 D—E). In Epiceratodus also there exists dorsally to the foramen of Monroi "a great brush of lateral choroidal infoldings (fig. 9, *l.ch.p.*), answering completely to the choroid plexus of the lateral ventricle in the Protopterus and selachian forebrain" (HOLMGREN, VAN DER HORST; 1925, p. 66).

If the conception, that the ependymatic part of the medial hemispheric wall in Epiceratodus constitutes a plexus choroideus lateralis is correct, then the choroidal folds, pointed out by HOLMGREN and VAN DER HORST, must be homologous to the plexus of the third ventricle in Protopterus. A comparison between their figs 8 and 9 and my fig. 29 D—E seems to strengthen this conception. HOLMGREN's and VAN DER HORST's lateral folds (*l.ch.p.*) have the same position as my plexus choroideus of the third ventricle (*pl.ch.III.*).

IV. TELENCEPHALIC CENTRES IN ADULT PROTOPTERUS AND THEIR DEVELOPMENT.

The forebrain of lungfishes is characterized by having a more or less homogenous ventricular cell-layer. The telencephalic centers are separated indistinctly from one another and maintain mostly their embryonic positions. Only exceptionally do they show a tendency to leave their matrix-layer in order to form distinct, migrated nuclei. In this the Dipnoans, especially Epiceratodus, resemble the Amphibians. Protopterus represents in some respects a more differentiated stage. As a result of the embryonic position of the telencephalic centres it is very difficult to fix their extension, especially as there exist only two boundary grooves which are constant in every specimen. In the lateral ventricular wall the pallium is limited ventrally by a sulcus limitans pallii lateralis. In the medial wall we have another groove, sulcus septalis, separating the two principle parts of the septal formation. As a result of the cellular arrangement, however, it is possible to distinguish the following centres in the adult forebrain of Protopterus:

A. Developing from the caudal telencephalic proliferation zone.

Pallium
Nucleus preopticus

B. Developing from the rostral (subpallial) telencephalic proliferation zone.

Bulbus olfactorius[1]
Nucleus olfactorius lateralis
Tuberculum olfactorium
Septum

BULBUS OLFACTORIUS.

Adult conditions.

The olfactory bulb of Protopterus is situated immediately in front of the dorsal parts of the hemisphere. The lateral parts of the bulb are extended ventrally and caudally. The parts on the medial side of the hemisphere occupies a relatively small space (fig. 21 A—D). The external, ventral boundary is determined by a fovea limbica. In a rostral direction this becomes very conspicuous and, frontally it appears as a powerful groove which separates the

[1] The olfactory bulb probably also contains elements pallial in origin (see p. 79).

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bulbar formation from the more ventrally situated subpallial parts (fig. 9 A—B). The fovea continues on the medial side where it is very soon obliterated. The external caudal boundary of the olfactory bulb consists of a sulcus limitans bulbii externus (*s.l.b.e.*, fig. 9 A—B). This groove constitutes an oblique, transversal sulcus between the caudal ends of the lateral and medial parts of the fovea. It is not always dinstinct along its entire extension, and is more pronounced in older than in younger specimens.

In the anterior part of the lateral ventricle there exist two rostral pockets, the dorsal of which penetrates into the bulbar formation (fig. 9 B). The latter is arched over this rudimentary bulbar ventricle. A transverse section, through the middle of the olfactory bulb, shows the anterior triangular part of this ventricle (fig. 21 A). The two ventral corners indicate the position of the lateral and medial parts of the sulcus limitans bulbi internus (*s.l.b.i.*, fig. 21 A).

Reading the sections in a caudal direction (fig. 21 A—D) one observes the dorsal displacement of the medial component of this boundary groove, which constitutes a ventricular correspondence to the external sulcus limitans bulbi externus. Caudally the bulbus olfactorius is restricted to the lateral hemispheric wall (fig. 21 C—D).

In the adult olfactory bulb of Protopterus the following elements are distinguishable:

Nervus olfactorius
Interglomerular cells
Glomeruli
Mitral cells
Fibre-layer
Granular layer

Nervus olfactorius.

The part of the olfactory nerve which is in contact with the forebrain has a cap-like structure, composed of coarse bundles. These are divided into a great number of slender fascicles (fig. 21, 22), which cross one another and send olfactory fibres to several glomeruli. Judging from the material at my disposal, the single olfactoy fibre does not branch outside the glomeruli and thus only enters one glomerulus. The same conditions also exist in bony fishes (Holmgren, 1920). In the anterior part of the olfactory bulb the bulk of the nerve bundles are located laterally and medially. On the dorsal side the nerve-layer is very thin. In the caudal part of the bulbar formation the nerve is situated laterally (fig. 21 A—D). According to Herrick (1924 b, 1931) there exists in Amphibians an "external limiting membrane", which the more slender fascicles and fila olfactoria have to penetrate before entering

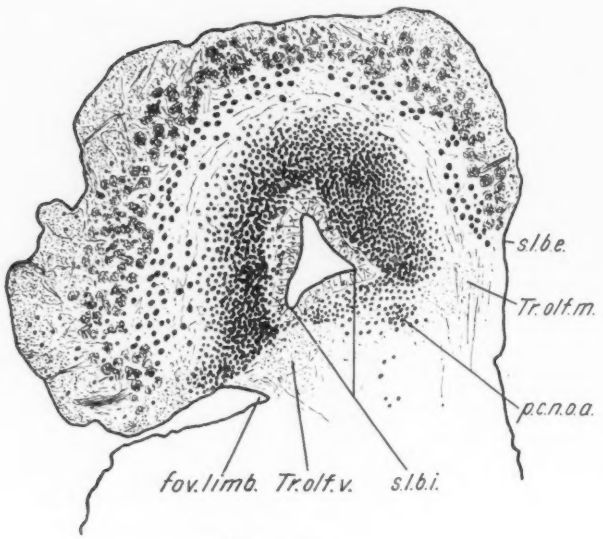

Fig. 21 A.

Fig. 21 A—D. *Protopterus annectens.* Adult forebrain. Transv. sect. indicated in fig. 9 B by the letterings 21 A—D. BIELSCHOWSKY, 56x.

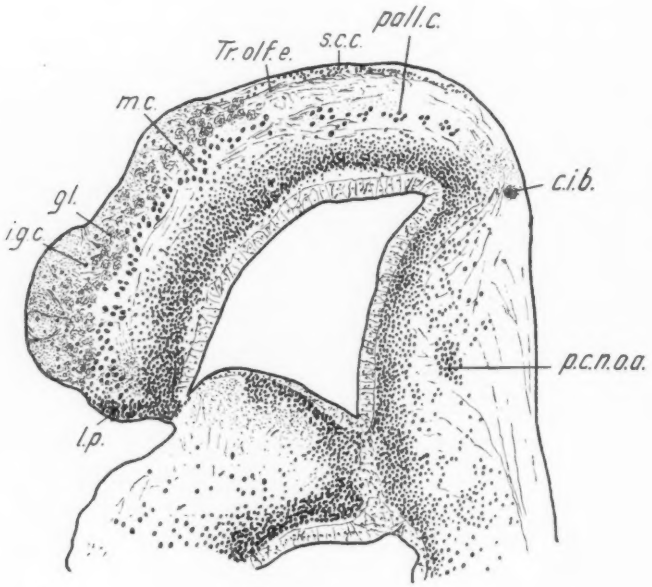

Fig. 21 C.

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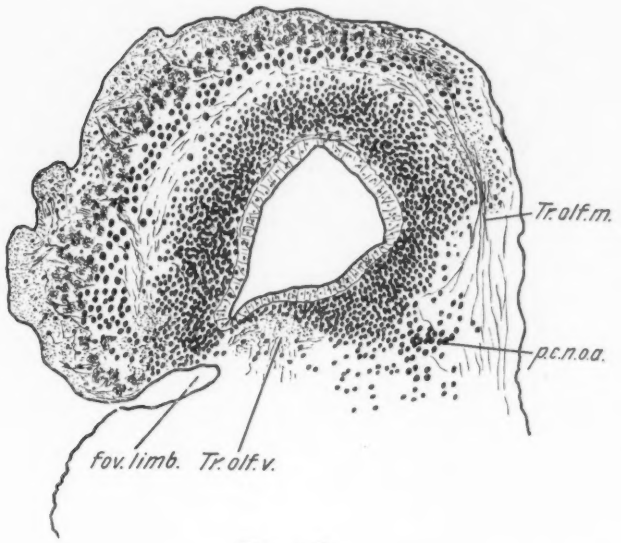

Fig. 21 B.

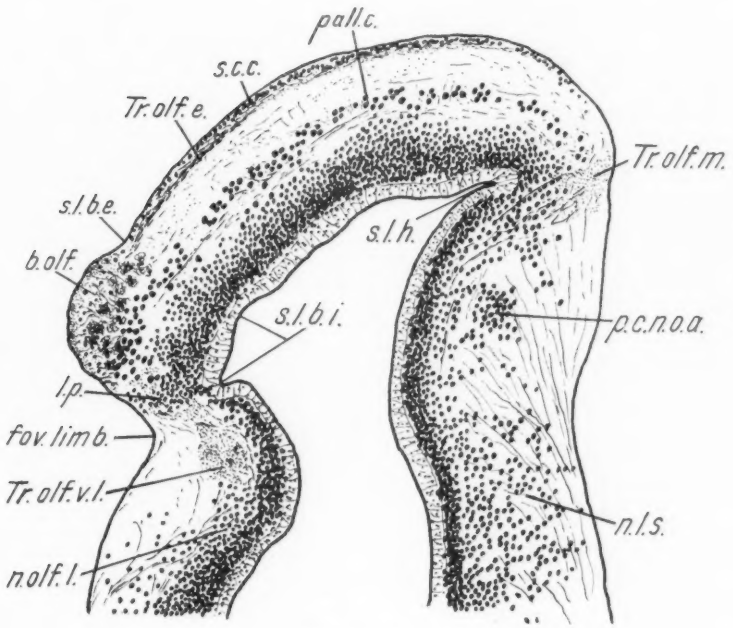

Fig. 21 D.

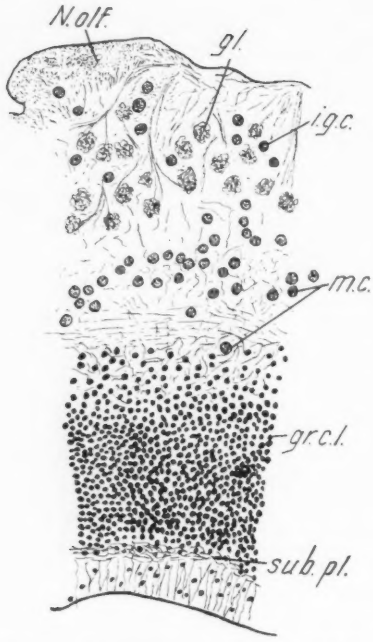

Fig. 22. *Protopterus annectens.* Adult forebrain. Transv. sect. through bulbus olfactorius. BIELSCHOWSKY, 70x.

the glomerular layer. I have not been able to observe any such structure in Dipnoans.

Interglomerular cells.

In the adult brain these cells do not constitute a distinct layer. They are scattered among the fila olfactoria and the glomeruli (*i.g.c.*, fig. 22). They usually have a short but coarse dendrite (fig. 23 A, C), which arborizes in a glomerulus. There also exist cells with two dendrites (fig. 23 B), or with a branched dendrite (fig. 23 E—F), and as a result of this the interglomerular cells may be connected to more than one glomerulus. The neurites start from the cell-body or from a dendrite. In a recent paper (RUDEBECK, 1944) I have mentioned that from the course of the neurites, it is possible to distinguish two types of interglomerular cells. In most of the cells the neurites assemble in the dorsal caudal part of the bulbus and here constitute a tractus olfactorius externus (*Tr.olf.e.*, figs 21 C—D, 23 A). Some cells, however, have neurites, which give off collaterales a short distance from the cell-body or the dendrite, and arborize in and among the glomeruli (fig. 23 D—E). According to HOLMGREN and VAN DER HORST (1925) somewhat similar conditions exist in Epiceratodus: "The preparations show very clearly that also neurites are entering the glomeruli. These fibres belong to the olfactory fibres of secondary orders, and are probably collaterales to neurites or neurites of mitral cells. These fibres split up in numerous branches, not only on the surface of the glomeruli, but also in their interior. So the mitral cells, to which these fibres belong, probably correspond with a kind of "interglomerular mitrals" as described in other vertebrates" (p. 88).

Glomeruli.

The glomeruli constitute a well defined layer in the external parts of the olfactory bulb, beneath the cap-like formation of the olfactory nerve. They consist of endbranches from olfactory fibres and from dendrites of interglomerular-, mitral- and granular cells. Golgi-preparations show the existence of two types of glomeruli. The one is built up by the endbranches of dendrites from the interglomerular cells. In the immediate vicinity of the glomerulus,

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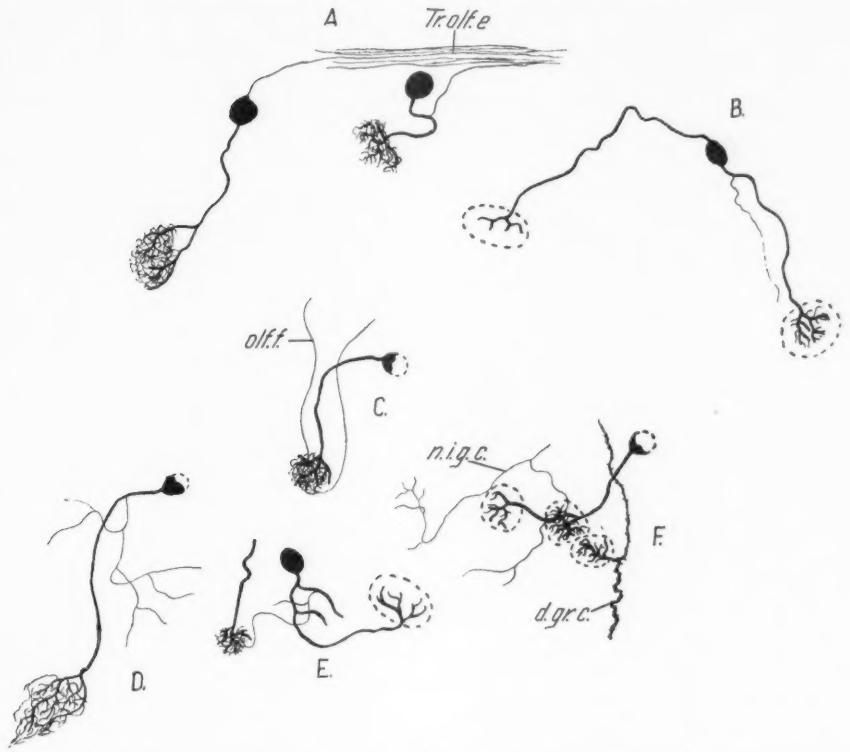


Fig. 23. *Protopterus annectens.* Interglomerular cells in the olfactory bulb. GOLGI, 200x.

the dendrite branches off in a few rather coarse ramifications, which divide into a very dense network of slender endbranches (fig. 23). The other type, which is built up by mitral dendrites, consists of coarse and not so densly packed endbranches (fig. 24 B—C). These two types are not always well pronounced as transitory structures exist. From the material it is evident, however, that the "mitral glomeruli" generally have a coarser structure than the "interglomerular glomeruli". Judging from HERRICK's (1931) figures the same conditions exist in Necturus.

Mitral cells.

These constitute a distinct layer immediately inside the glomeruli. In sections stained by BIELSCHOWSKY's method they are easily recognizable by their light colour. Such cells also appear in the fibre-layer and externally among the granular cells. In Golgi-preparations the mitral cells show very long, coarse, often branched but smooth dendrites. In fig. 24 A—C some of the different types of mitral cells are drawn. A shows a more unusual form with one short dendrite. After the neurite leaves the cell-body, I have been able to follow

it a short distance into the fibre-layer outside the granular layer. Another type with several dendrites leaving the cellbody is shown in B. The most common type is seen in C. These cells have a short principal dendrite which very soon branches off in a number of ramifications, some of which are very long. The neurites in most of these cells start from the cell-body, and enter the fibre-layer. According to my observations, there exist no collaterales to mitral neurites inside the bulbar formation with the exception of a doubtful case consisting of a cell in the mitral layer beneath the glomeruli, which has a neurite continuing down to the fibre-layer, and sending off a collateral to the superficial, anterior part of the olfactory bulb (fig. 24 G) just after leaving the cell-body. This is the only case of mitral neurites sending off collaterales inside the bulbar formation which I have been able to observe. This structure may represent an interglomerular cell, which has been pushed down ventrally and been placed inside the mitral layer. According to HOLMGREN, no endbranches or collaterales of mitral neurites exist inside the bulbar formation in fishes. They do, however, exist in Urodeles (HERRICK, 1924 b).

KIESEWALTER (1928) states that "wir im Laufe der Phylogenie eine Verlagerung der Mitralzellen auf die einlaufenden Reize zu werden beobachten können. In der Tat sehen wir bei den höheren Vertebratenklassen, von den Reptilien an, dass die Mitralzellenschicht, den periventrikulären Körnern, durch eine zellfreie Zone geschieden ist..... Es ist das Verdienst Kuhlenbecks, nachgewiesen zu haben, dass diese Verlagerung der Mitralzellen bereits bei den höchst organisierten Ordnung der Amphibien, bei den Coeciliern, eingetreten ist" (p. 405). According to KUHLENBECK (1922 a) these conditions also exist in Anura. But this cell-free zone is already very distinct in Dipnoans and in bony fishes (HOLMGREN, 1920).

The fibre-layer.

This layer contains neurites from mitral and granular cells. Mingled with these are dendritical branches from the latter. Medially and dorsally the fiber layer at the caudal border of the bulbar formation passes uninterruptedly over into the white matter of neigbouring parts of the hemisphere. In the lateral parts, on the other hand, this layer is cut off ventrally by a cell-prominens which extends between the granular layer and the mitral cells (*l.p.*, fig. 21 C—D).

Granular cells.

The granular (ventricular) layer of the olfactory bulb is situated dorsally, laterally and in front of the bulbar ventricle (fig. 21 A—D). Caudally this layer passes over into the ventricular layer of the pallium. In this latter part the cellular arrangement is the same as in the granular layer of the bulb. The only structure which marks the limit between these parts is the sulcus limitans bulbii internus.

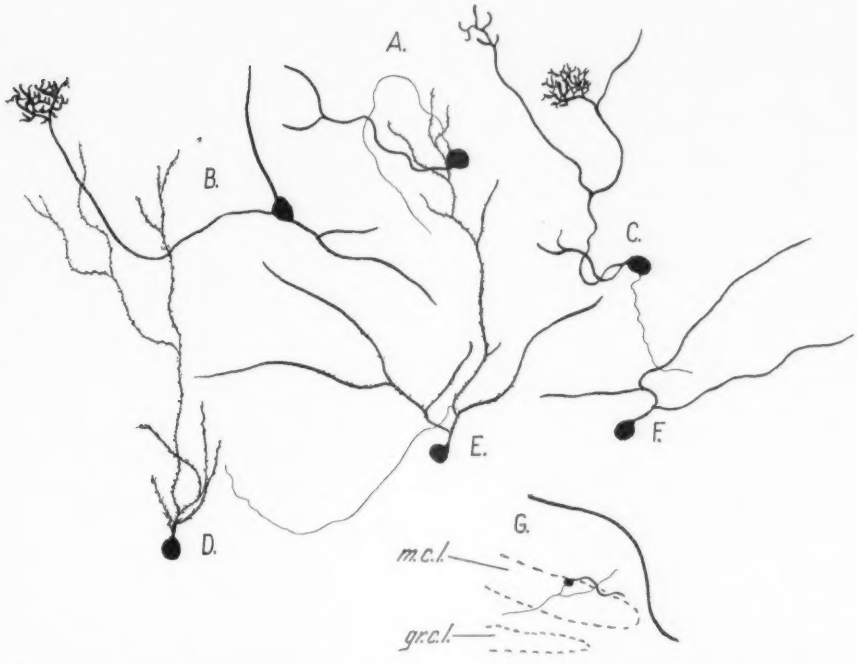


Fig. 24. *Protopterus annectens.* Cell types in the olfactory bulb. GOLGI; A—F 200x, G 100x.

In my Golgi-preparations the dendrites, unlike the cell-bodies, are easily stained and appear very often as thicket-like structures. The most common type of cells has a short principal dendrite, which arborizes in a great number of long, slender branches extending up in the external layers of the bulbar formation. Their endbranches lie among the glomeruli, or contribute to the building up of these structures. The dentritical branches are more or less spiny or mossy. These cells constitute the bulk of the granular layer. In the external parts there exist cells with a somewhat different appearance.

Fig. 24 D shows a cell which does not differ very much from a common granular cell. The principal dendrite is often somewhat longer and coarser, and the dendritical branches are less numerous. In another type of cell the dendritical branches spread over a greater area (fig. 24 E), and are not pressed against one another, which is a typical feature of most of the granular cells. In the most external parts of the granular layer the preparations show cells which do not differ in any way from the mitral cells. The dendrites are long, smooth and widely spread (fig. 24 F). They often run a distance parallel to the surface of the granular layer before turning off towards the glomerular layer. These cells probably represent mitral cells which have not migrated, but have been left in their matrix layer. As has been the case in the Bielschowsky-

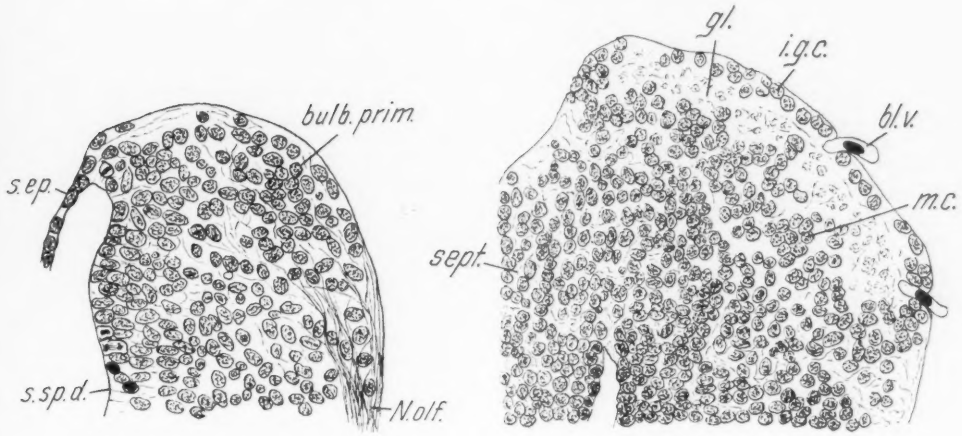
preparations mentioned above, we find cells in this part which have the same appearance as the migrated mitral cells.

Development.

The structure of the olfactory bulb in its principal parts is analogous to the same formation in other fishes (see HOLMGREN, 1920), with the exception of the presence of interglomerular cells in Protopterus. The mitral cells constitute a well defined layer homologous to "Die Schicht der grösseren Mitralzellen" in Osmerus, and as in this form, the neurites from this layer leave the bulbar formation without giving off collaterales or endbranches to the glomerular layer. The cellular elements in Protopterus seem to be more uniform than in bony fishes. This applies especially to the granular layer (nucleus olfactorius anterior in Osmerus).

In Stage 4 the cellular elements of the bulbus olfactorius begin to differentiate. The olfactory nerve enters the hemispheric primordium dorsally at the border between the pallial and subpallial proliferation zones (*N.olf.*, *b.olf.*, fig. 4 A, D). In this part there exists a cellular condensation external to the ventricular cell-layer (*bulb.prim.*, fig. 25 A). Olfactory fibres penetrate between the cells of this structure and those internal to it. During the development, glomeruli begin to appear in the external layer of this primordium and as a result, most of the cells are forced inward against the ventricular layer. A thin row of cells, however, is left on the surface. In Stage 5 this external layer, the interglomerular cells (*i.g.c.*, fig. 25 B), are separated distinctly from the underlying, much thicker layer of mitral cells (*m.c.*, fig. 25 B). The fibre layer of the olfactory bulb is as yet very inconspicuous, but during the subsequent development it becomes more and more accentuated and separates distinctly the mitral cells from the underlying granular layer.

The development shows that the interglomerular cells constitute a layer of superficially placed mitral cells, some of which are characterized by having a neurite which arborizes inside the glomerular layer. In these conditions the Dipnoans differ from other fishes, and show structures characteristic of Amphibians and higher vertebrates. From HERRICK's investigations on the Urodela (1924 b, 1931) it is evident that the above mentioned interglomerular cells of Protopterus correspond to the periglomerular cells of Amblystoma and Necturus. HOLMGREN (1920) is of the opinion that, "In der Phylogenie der Tetrapoden scheint eine Veränderung der oberflächlichen (interglomerularen) Mitralzellen stattgefunden zu haben, indem diese bei den Säugetieren zu intra- und peri-glomerularen Zellen sich veränderten, indem der Axon sich nicht länger mit dem Tractus olfactorius lateralis vereinte, sondern kurz bliebe um ein Assoziation zwischen den Glomeruli zu besorgen" (p. 19). The peri-



A. B.

Fig. 25 A—B. *Protopterus annectens.* Transv. sect. through the primordium of the bulbus olfactorius in Stage 4 (A, 12.4 mm) and Stage 5 (B, 15 mm). AZAN-MALLORY, 150x.

glomerular elements in Protopterus show that this transformation has already occured in Dipnoans.

HOLMGREN and VAN DER HORST (1925) state that in Epiceratodus the bulbar formation holds a position dorsal to the fovea limbica. "The fovea may in the adult brain roughly correspond with the exterior boundary between the pallial and subpallial parts. Thus the olfactory apparatus seems to have chiefly pallial position in the adult" (p. 64). According to the same authors, however, GREIL's (1913) investigation argues against this. "GREIL, however, has shown that the olfactory nerve in the embryo enters the lateral, probably subpallial part of the forebrain".

As is evident from the ontogenetic development, the olfactory nerve enters the subpallial area of the telencephalic primordium. The different elements of the olfactory bulb, however, do not begin to differentiate until this entrance has undergone a dorsally directed displacement and becomes situated immediately in front of the anterior parts of the pallial primordium. In the above mentioned paper (RUDEBECK, 1944) I have described some structures in these parts of the pallium which may be the forerunners of an accessory olfactory bulb, and I have also mentioned the great similarity in the development between anterior parts of the pallial cortex and the mitral- and interglomerular layers in the bulbus olfactorius. These conditions seem to me to indicate that the olfactory bulb at least partly develops out of the pallial primordium.

HOLMGREN (1925) has shown the pallial origin of the accessory olfactory bulb in reptiles and mammals, and he points out that it is not out of the question that the olfactory bulb in fishes represents a pallial derivative.

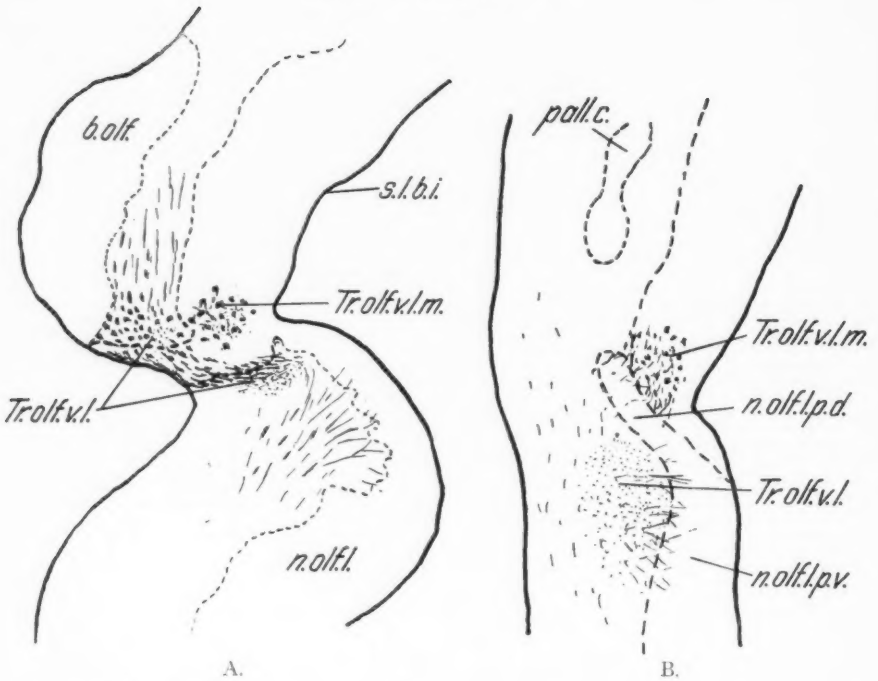


Fig. 26 A—C. *Protopterus annectens.* Adult forebrain. Transv. sect. through the rostral parts of the lateral hemispheric wall. BIELSCHOWSKY, 52x.

"A cursory examination of developmental stages of Amia seems to indicate that the pallial derivation of the bulbar formation is not excluded" (p. 449). These conditions make HOLMGREN question whether it is not "possible that the nasal sac of bony fishes represents the vomero-nasal organ and that the bulbus olfactorius consequently should be the vomero-nasal formation?". The conditions in Protopterus argue somewhat against this theory. It would signify that the highly developed and differentiated olfactory bulb in Protopterus was quite a new structure, not comparable with the same formation in other fishes, as structures exist in this species, pallial in origin, which in all probability should be interpreted as an accessory olfactory bulb (RUDEBECK, 1944). The latter structure would thus be a remaining rudiment of the olfactory bulb in other fishes.

Tractus olfactorius.

From the fibre layer of the olfactory bulb, fibres stream over into the neighbouring parts of the pallium and the subpallium. These fibres constitute a t r a c t u s o l f a c t o r i u s, the different components of which are separated

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indistinctly from each other. From an investigation of preparations made by WEIGERT's method, it is evident that the myelinated elements in the fibre-anatomical structures in telencephalon of Protopterus are very few in number. In the lateral components of the olfactory tract there exist some myelinated fibres. According to HOLMGREN and VAN DER HORST the same conditions exist in Epiceratodus.

Those fibres, which leave the bulbus dorsally and laterally, constitute a tractus olfacto-dorsolateralis, which spreads over the pallial formation. This tractus contains unmyelinated elements and divides into an external and internal layer one on each side of the pallial cortex (*Tr.olf.d.l.*, fig. 27).

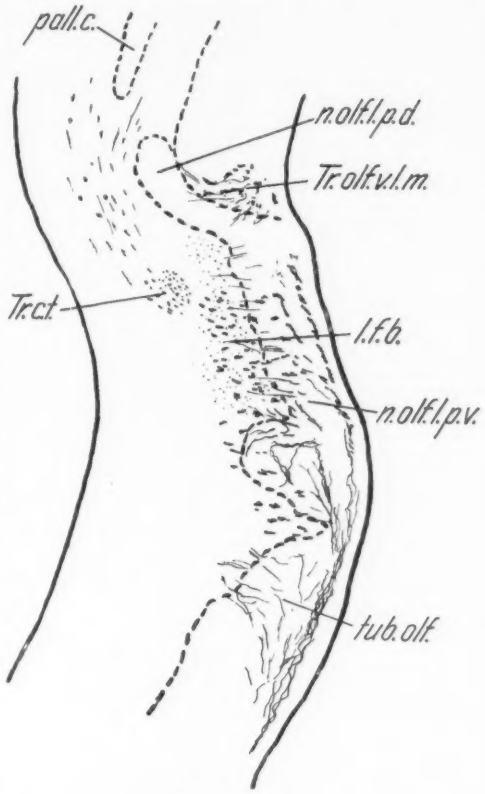

Fig. 26 C.

Ventrally and laterally secondary fibres assemble and constitute a tractus olfacto-ventrolateralis (*Tr.olf.v.l.*, fig. 26 A). From this, fibres penetrate through the lateral prominentia of the granular layer of the olfactory bulb and assemble ventrally to this outside the dorsal, anterior parts of the lateral olfactory nucleus (fig. 26 A). Tractus olfacto-ventrolateralis, which contains some myelinated elements, connects the olfactory bulb with this nucleus and with the dorso-lateral parts of the tuberculum olfactorium. In its anterior parts only, immediately after leaving the bulbar formation, it constitutes a rather well defined tract. Very soon, however, the fibres begin to disperse in the lateral and dorso-lateral parts of the subpallial formation. The tract in question has a medial component which is situated among the cells in the ventro-lateral parts of the granular layer (*Tr.olf.v.l.m.*, fig. 26 A). This tractus olfacto-ventrolateralis medialis continues caudally where it holds a position between the pallium and the lateral olfactory nucleus (*Tr.olf.v.l.m.*, fig. 26 B—C). It sends out fibres to the dorsal parts of this nucleus and to the ventro-lateral parts of the pallial formation. This medial component of the ventro-lateral olfactory tract seems to correspond to HOLMGREN's and VAN DER HORST's "pyriform tract" in Epiceratodus. Among the

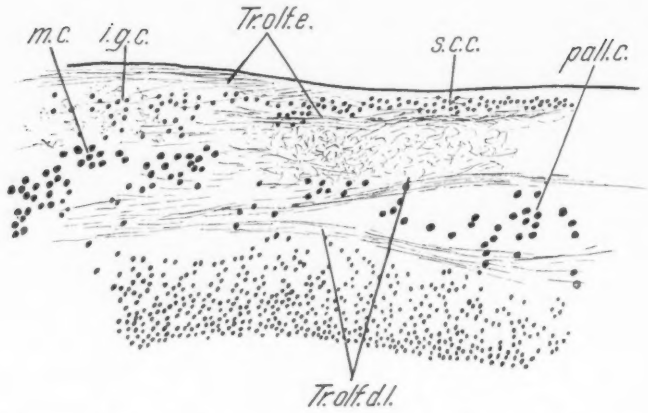

Fig. 27. *Protopterus annectens.* Adult forebrain. Sagittal sect. through the border region between the pallium and the bulbus olfactorius. BODIAN, 25x.

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myelinated elements in the ventro-lateral tract I have been able to follow some fibres to the caudal parts of the hemisphere, and here they mingle with the dorsal elements of the lateral forebrain bundle. Immediately caudal to the level of the foramen of Monroi, some of the myelinated elements from this part of the bundle enter the stria medullaris. Probably some of these belong to the myelinated elements of the tractus olfacto-ventrolateralis and constitute a tractus olfactorius lateralis habenulae, which also exists in Epiceratodus.

Those fibres which stream down from medial parts of the olfactory bulb into the septal formation constitute a tractus olfactorius medialis (*Tr.olf.m.*, fig. 21 A, D). Among these medial olfactory fibres appears a rather well definded bundle which is located in the dorsal parts of the medial hemispheric wall (*c.i.b.*, figs 21 C, 28). In the caudal half of this wall it turns down ventrally and is situated externally in the septal fibre layers. The bundle continues ventrally and caudally and finally crosses into the most dorsal portion of the anterior commissure and then enters the medial wall of the opposite hemisphere. This bundle corresponds to the commissura interbulbaris of Epiceratodus.

The rostral subpallial parts, ventrally to the bulbar formation, receive secondary olfactory fibres by means of a tractus olfactorius ventralis (*Tr.olf.v.*, fig. 21 A—B).

As already has been pointed out, these different components of the olfactory tract are indistinctly separated from one another, with the exception of the interbulbar commissure. According to HOLMGREN and VAN DER HORST, the corresponding conditions exist in Epiceratodus. "So at the frontal end of the hemispheres there is no single fibre complex constituting a fibre unity."

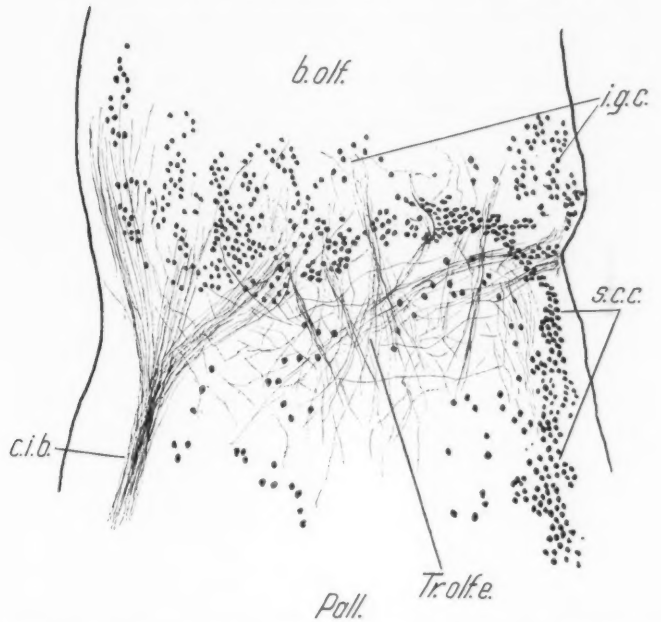

Fig. 28. *Protopterus annectens.* Adult forebrain. Horizontal sect. through the border region between the pallium and the bulbus olfactorius (lateral parts to the right). BODIAN, 30x.

There exists, however, another very well defined fibrous structure in the olfactory bulb in Protopterus, which I already have described in connection with the discussion of the accessory olfactory bulb, i. e. the tractus olfactorius externus. This is easily distinguished in preparations stained by the BODIAN's and BIELSCHOWSKY's methods (*Tr.olf.e.*, figs 21 C—D, 27—28). This tract which contains the neurites from the bulk of the interglomerular cells does not reach beyond the anterior third of the pallium (RUDEBECK, 1944).

HOLMGREN and VAN DER HORST have shown the existence of a very powerfully developed subependymal plexus in the bulbar formation and olfactory crus of the Epiceratodus. In Protopterus such a plexus exists but is very inconspicous (*sub.pl.*, fig. 22). The subependymal fibres assemble in the ventrolateral parts of the bulb. Here they join the medial component of the ventrolateral olfactory tract.

PALLIUM.

Adult conditions.

Pallium occupies a relatively small space in the dorso-lateral parts of the hemisphere, caudally to the bulbar formation. The ventral ventricular boundary is de-

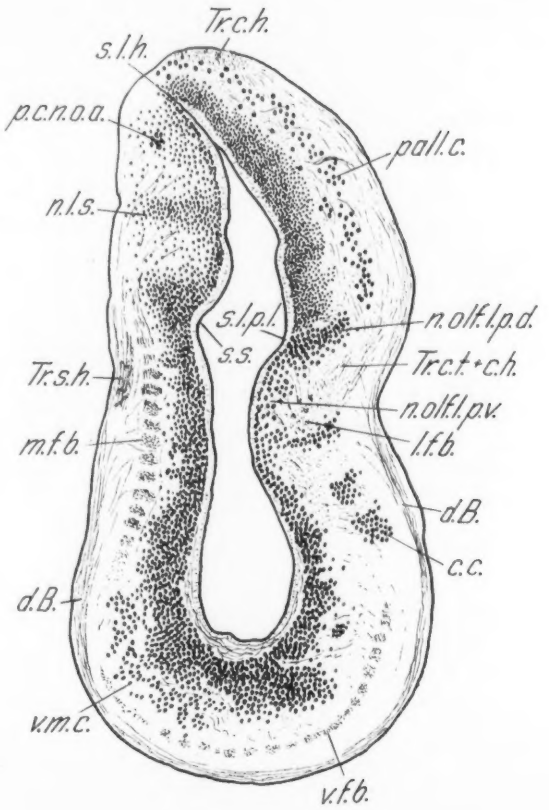

Fig. 29 A.

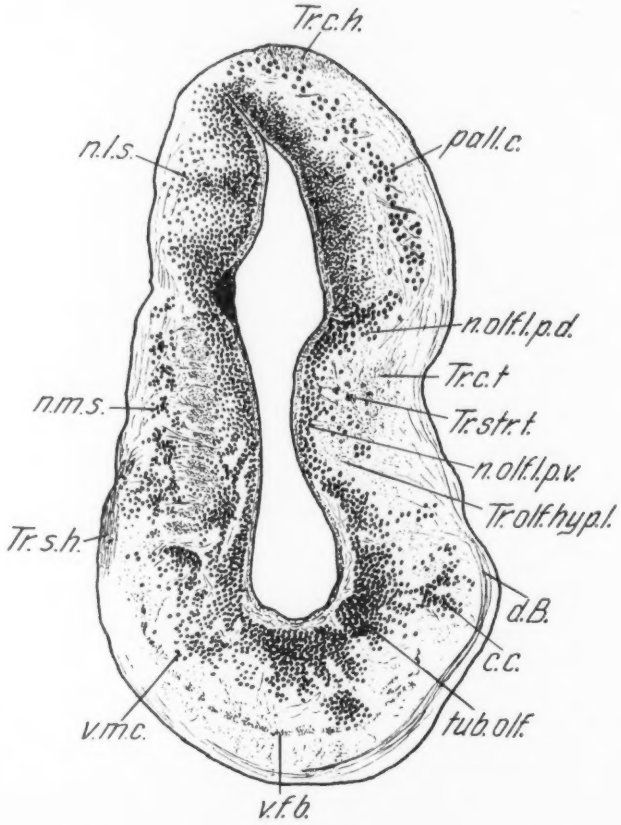

Fig. 29 B.

Fig. 29 A—G. *Protopterus annectens.* Adult forebrain. A—F transv. sect. indicated in fig. 9 B by the letterings 29 A—F; 21x. G sag. sect. through commissura anterior; 75x. BIELSCHOWSKY.

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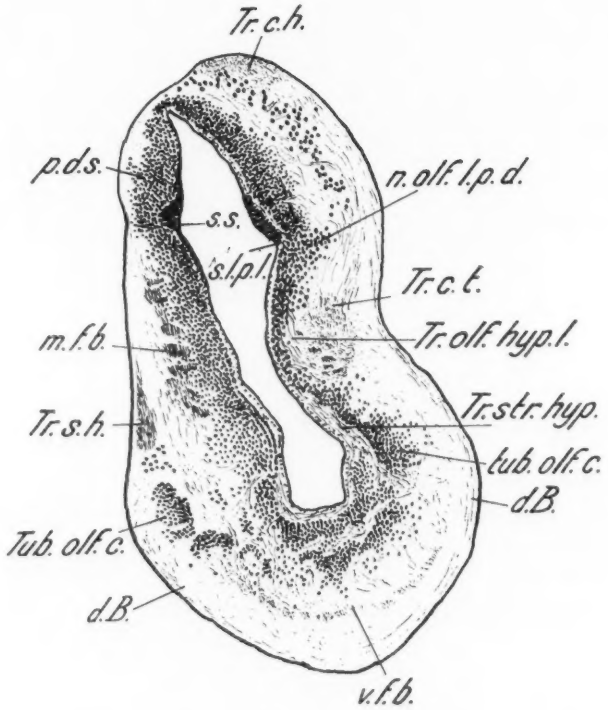

Fig. 29 C.

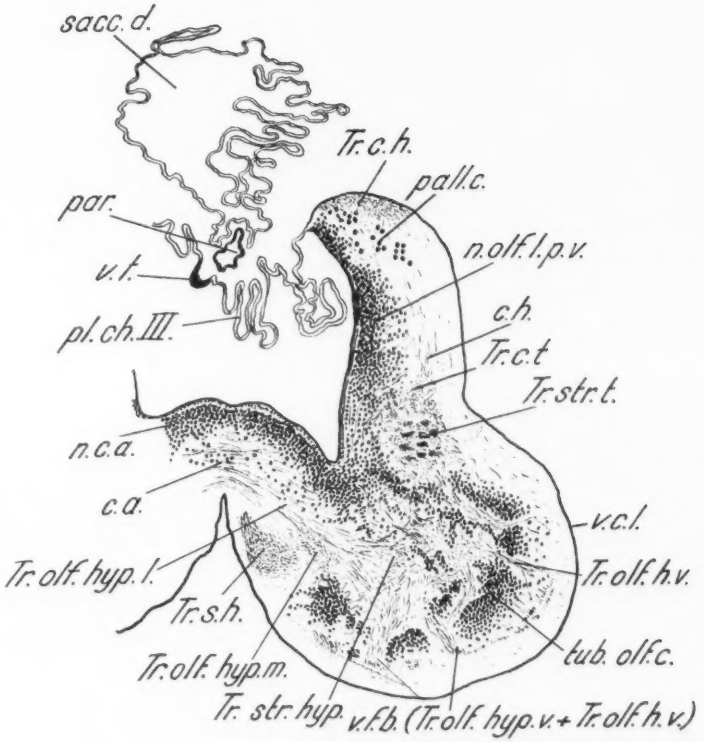

Fig. 29 D.

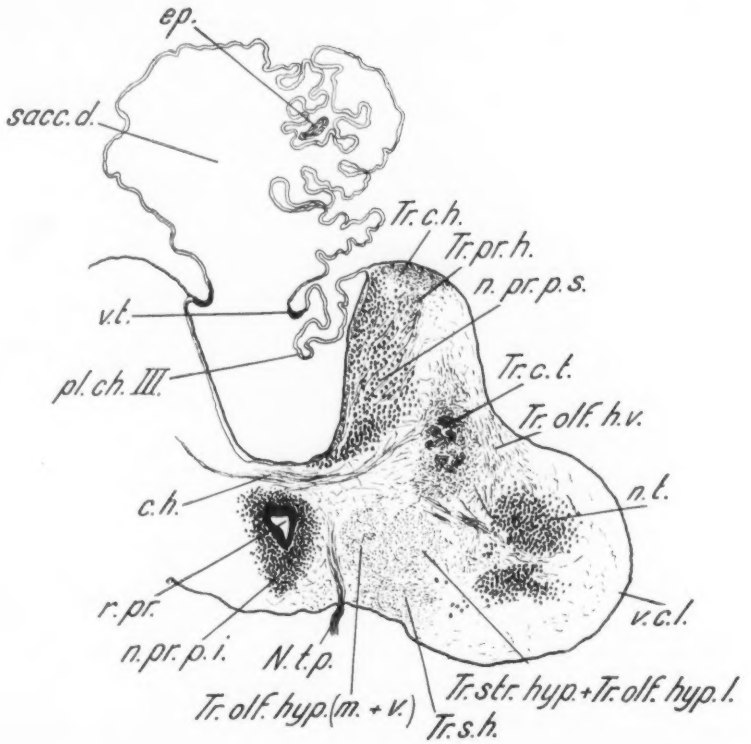

Fig. 29 E.

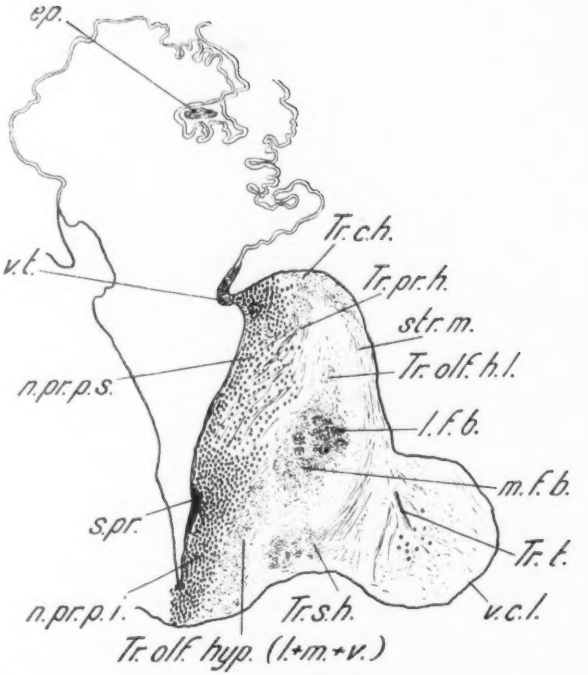

Fig. 29 F.

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lineated by the sulcus limitans pallii lateralis, which in its caudal parts is powerfully ependymated (*s.l.p.l.*, fig. 29 A, C). The medial (dorsal) ventricular boundary is marked by the angulus dorsalis of the lateral ventricle. Pallium thus does not constitute any part of the medial hemispheric wall. Distinct zonae limitantes do not exist, but the ventricular cell-layer is easily distinguishable from the subpallial parts because of the small, densely packed and darkly stained cell-nuclei. In the caudal parts of the hemisphere the extension of the pallial structure diminishes, and immediately caudal to the level of the foramen of Monroi, the pallium, in the dorsal parts of telencephalon, is replaced by the pars superior of the preoptic nucleus (fig. 29 A—F).

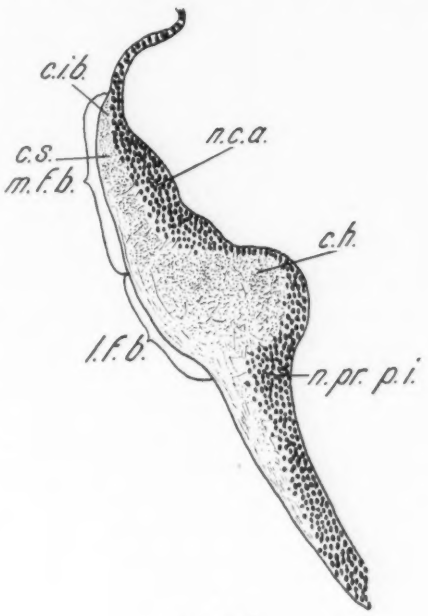

Fig. 29 G.

In the pallium of Protopterus the following layers are distinguishable:

Ventricular cells
Internal fibre layer
Cortex
External fibre layer
Supracortical cells (in the anterior third of the hemisphere)

Ventricular cells.

The ventricular layer of cells appears as a uniform structure, which is distinctly thinner at its dorsal and ventral borders (fig. 29 A—B). It is not divided into any distinct areas, and except for the dorsal and ventral boundary grooves, no constant sulci appear in this part of the hemisphere.

My Golgi-preparations show three different kinds of cells. The cell-type building up the bulk of the ventricular layer resemble very much in structure the granular cells of the olfactory bulb. They have a very short principal dendrite, which arborizes in a dense bunch of rather slender but very mossy branches (fig. 30 A). Most of these extend up into the external fibre layer. Some of them seems to end in the cortical layer.

Among these cell-elements I have found a few cells characterized by having a rather long principal dendrite, which arborizes in a fairly widespread area. The dendrite and its branches are very slender (*v.p.c.*, fig. 30 B), and the

latter end in the external fibre layer and among the cortical cells. The neurite seems to enter the cell-layer in a ventricular direction. Possibly some of the fibres in the slightly developed subependymal plexus contains neurites from these cells. Since I have only been able to follow the neurites a short distance, however, I have no accurate conception concerning their course.

The third cell-type is found in the external parts of the ventricular layer, especially in its thickened, dorso-lateral part (*v.c.c.*, fig. 30 B—C). These cells correspond in every respect to the cells of the pallial cortex with their long, thick but smooth dendrites. They probably constitute cortical cells left behind in their matrix layer (cf. the conditions in the olfactory bulb with regard to the mitral cells and the cells in the external part of the granular layer; p. 77).

In preparations stained by BIELSCHOWSKY's method we find these ventricular cortical cells in the outer parts of the ventricular layer and in these preparations they have the same light colour as the real cortical cells. These preparations also show that they are more numerous in the dorso-lateral parts of the ventricular layer. Outside this layer ventricular cortical cells appear here and there in the internal fibre layer.

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Internal fibre layer.

This layer contains fibres belonging to the dorso-lateral olfactory tract, and neurites from the ventricular and cortical layers. The fibres have a tendency to assemble in distinct bundles, which run a short distance in a caudal direction before turning lateralwards and breaking through the pallial cortex into the external fibre layer. In this part the bundles turns caudally and split up into single fibres. In the internal layer there also exist collaterals from cortical and ventricular cortical neurites (fig. 30 C). In Bodian-preparations I have found endbranches of fibres which have been possible to follow down into subpallial fibre layers outside the lateral olfactory nucleus. Besides neurites and endbranches and collaterals to neurites the internal layer contains dendritical branches from ventricular and ventricular cortical cells.

Cortex.

The pallial cortex constitutes a distinct, more or less dorsoventrally extended lamina, which in younger specimens is somewhat thicker in the dorsal and ventral parts. In Bielschowsky-preparations the cortical layer appears as lightly stained cells gathered into clusters, separated by the above mentioned fibre bundles, passing from the internal to the external fibre layers. The dendrites are very long, thick and smooth, and run parallel to the cortical layer. From these dendrites branches go out towards the hemispheric surface. They arborize in the external fibre layer. The neurites which often contain collaterals are found in both the external and the internal fibre layer.

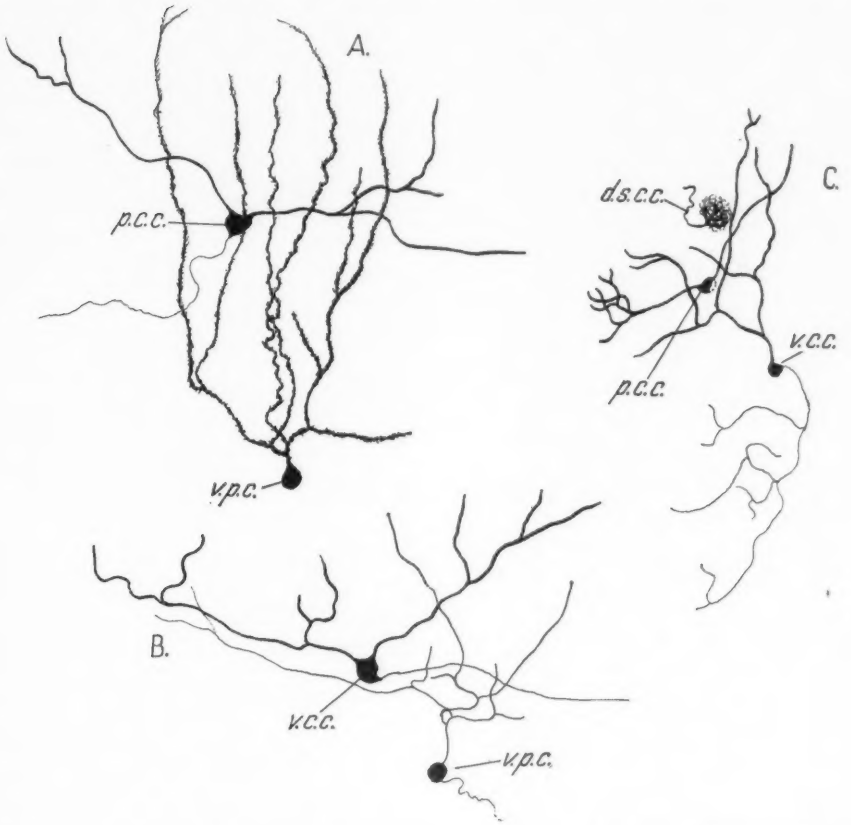

Fig. 30. *Protopterus annectens.* Adult forebrain. Cell-types in pallium. A—B 200x; C 150x. GOLGI.

External fibre layer.

This contains secondary olfactory fibres belonging to the tractus olfactodorsolateralis. In the anterior third of the pallial formation there exist fibres from the tractus olfactorius externus. To these elements are added neurites from cortical and supracortical cells, together with dendrites and dendritical branches from all cellular parts of the pallium. In the external layer are located most of the pallial fibre connections with other brainparts.

Supracortical cells.

These cells I already have treated in my paper dealing with the probable existence of an accessory olfactory bulb in Protopterus, and for details concerning the structure and significance of this superficial pallial cortex the reader is refered to that paper (RUDEBECK, 1944). These cells probably repre-

sent a bulbar structure as they have dendrites which arborize into glomerulilike structures. As far as I can see the neurites do not leave the pallial formation but arborize among the end branches of dendrites from cortical and ventricular cells.

BURCKHARDT (1892 b) divides the hemisphere of the Protopterus into three zones, "Ventralzone, Medialzone" and "Dorsalzone". The latter consists according to Burckhardt "aus Centralgrau und weisser Substans. Diese enthält (Figg. 21—25) eine Hirnrinde (I. Zsch) und ausserdem in ihren dorsalen vorderen Regionen eine äusserste Zellenschicht (A. Zsch). Sie ist der ganze länge nach gegen die Ventralzone hin durch eine deutliche Furche abgetrennt. Grenzen: α und γ" (p. 26).

BURCKHARDT's dorsal zone corresponds to pallium, limited dorsally by the angulus dorsalis of the lateral ventricle (α) and ventrally by sulcus limitans pallii lateralis (γ). "Centralgrau" is the same as the ventricular cell-layer. He has an "innere Zellenschicht der Grosshirnrinde" which is the cortex, and he has also observed the supracortical cells, "äussere Zellenschicht der Grosshirnrinde". As ELLIOT SMITH (1908) has pointed out, BURCKHARDT has made an error in including the olfactory bulb in the dorsal zone. According to the latter, the bulb "der Riechschleimhaut unmittelbar anliegt". The "innere Rinde" thus contains the mitral cells, and "die äussere Rinde" the interglomerular cells (see his figs 24—26, T. III).

ELLIOT SMITH (1908) states that in Lepidosiren "there can be no hesitation in recognising the formatio pallialis as a true pallium, the medial part of which is certainly homologous with the hippocampus of the Reptilia and Mammalia". Elliot Smith points out that he cannot fix any boundary between the hippocampal and pyriform component, or whether there exists a neopallial part interposed between them. "We ought rather to look upon the pallium of Lepidosiren as an area which is yet unspecialised, the rudiment of that more extensive cortical field which in the Mammalia becomes differentiated into distinct formations" (p. 529).

HOLMGREN (1922) points out that in Protopterus "the primordial cortex" has an "indistinct thickening at each side", and further on he states that the ventricular layer "at the upper end of the ventricle is very thick, protruding against the thinner part of the cortex". He also remarks that this structure "reminds one of the general pallium rudiment in Acanthias" (p. 418). As is evident from the figures in ELLIOT SMITH's paper the dorsal and ventral thickening of the pallial cortex in Lepidosiren are rather conspicuous. In adult brains of Protopterus they are very indistinct. They are more pronounced in larval stages. As in Protopterus the dorso-lateral thickening of the ventricular layer is very distinct in Lepidosiren.

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GERLACH (1933) distinguishes three areas in the ventricular cell-layer of Protopterus, a thick dorsal and two thinner, situated laterally. He states that the dorsal D_3 is separated from the lateral D_2 by a groove, fd_3. The lateral areas are separated by a caudally distinct sulcus fd_2. The cellular arrangement is said to be the same in both these areas, but in the dorsal area the cell-nuclei are stained and arranged differently.

No doubt there exist grooves in the pallial parts of the ventricular wall in some of the forebrains of Protopterus investigated by me, but with the exceptance of the dorsal and ventral boundary grooves, they must be considered as artefacts. They do not appear in all specimens and can be situated in all parts of the ventricular wall. They are very short and in no case have I found any such groove extending from the anterior to the posterior part of the pallial ventricular wall. GERLACH does not make clear the nature of the different arrangement of the cellular structure in the dorsal and lateral parts of the ventricular cell-layer, and I have not been able to observe any difference. The only structure that could be advanced in support of a difference, is the dorso-lateral thickening of the ventricular layer and which contains the lateral parts of GERLACH's D_3 and the dorsal parts of D_2. The cellular structure, however, is uniform throughout the whole layer and it is only the existence of a greater number of ventricular cortical cells in the outer layer of the thickened part which distinguishes it from the dorsal and ventral areas. GERLACH is of the opinion that the dorsal and ventral parts of the pallial cortex are in contact with the ventricular layer. In the dorsal part of the pallial formation, no fusing exists between the cortex and its matrix layer, but single cortex cells may appear in the internal fibre layer here as well as in other parts. Nor do the ventral parts of the cortex have any contact with the ventricular layer. Certainly a dorso-laterally directed prominentia from this layer juts out towards the cortex, but as is evident from the size and arrangement of the cells, this is a subpallial structure, and is also well separated from the pallial cortex by means of a cell-free zone (*n.olf.l.p.d.*, fig. 29 A—C).

The pallial ventricular layer in Epiceratodus is divided into three parts according to HOLMGREN and VAN DER HORST (1925, p. 70—71) "The hippocampal part is caudally not sharply separated from the general pallium but on a more frontal level there is a slight depression at the boundary of these two pallial parts. The differences are, however, sufficiently great to allow the conception of the two parts as being of different nature". Concerning the general pallial part the authors state that "the ventricular cell layer of this brain part is much thicker that in other parts, with scattered cells between it and the wandered out magnocellular cortex layer". The pyriforme lobe "is well delimited from the general pallium, as the ventricular layer of this brainpart in the Stockholm specimen is much thinner than that of the general pallium. In the older Amsterdam specimen the limit is not so distinct, the layer not being

thinner, but the arrangement of the cells being more diffuse than in the general pallium". The pallial cortex is built up as in Protopterus. "This layer consists of rather great cells, which are arranged as to form a distinct cortical layer. This layer is perfectly continous with that of the hippocampal and pyriforme lobe. Thus there are no limits corresponding with the limits of the ventricular pallial layers. The cortex layer is to be regarded as a primordial cortex, and therefore no limits ought to be present".

The statements citied above show that the pallial formation is principally of the same structure in the mono- and dipneumonian lungfishes. The only difference is that it is possible to distinguish the extension of the hippocampal-, neopallial- and pyriform components in the ventricular layer in Epiceratodus. As in Protopterus, the pallium of Epiceratodus does not constitute a part of the medial hemispheric wall.

The development of the pallial cortex.

This structure begins to differentiate between Stage 4 and 5, and at first appears as an indistinct thickening of the external layers of the ventricular cells in the dorso-lateral and caudal parts of the hemispheric primordium (*pall.c.*, fig. 31 A). In Stage 5 this thickening has distinctly separated from the ventricular cells and appears as a lamina with irregularly arranged cells (*pall.c.*, fig. 31 B). In the most dorsal part, immediately below the hemispheric surface, a few cells constitute a thin superficial string of cells (*s.c.c.*, fig. 31 B), which represents the supracortical lamina. The lateral parts of the pallial cortex, the pyriform component, very soon begin to be more accentuated, especially in somewhat older stages (*p.c.*, fig. 31 C). A parasagittal section through the caudal parts of the hemispheric primordium in such a stage shows the cortical lamina as a crescent-shaped structure, wholly defined to the caudal hemispheric lobe (*p.c.*, fig. 5 RUDEBECK, 1944). In the stages treated above this lamina is situated in the dorso-lateral parts of the lateral hemispheric wall. In Stage 7 the pallial cortex has a more dorsal position, and is situated partly in the medial dorsal parts of the hemisphere. The medial and lateral components of the cortex are more pronounced (*h.c.*,*p.c.*, fig. 31 D), and are connected to each other by a thin row of cells. The ventricular cell-layer protrudes against this latter part from beneath. In the internal fibre layer scattered cells appear, partly filling up the space between these structures.

HOLMGREN (1922) has shown that in all groupes of fishes there exists a pallium which contains a more or less differentiated cortical structure. The pallium is subdivided into a medial hippocampus, a lateral pyriformis and interposed between them a general pallium. HOLMGREN has investigated the ontogenetic development of the pallium in Acanthias, and according to him, the first cortical structure to appear is a primordial cortex, which is "prac-

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Fig. 31 A—D. *Protopterus annectens.* A 12 mm, transv. sect. through pallial primordium; 135x. B—C transv. sect. at the level of the foramen Monroi; B 15 mm, 75x; C 20.2 mm, 60x. D 55 mm, transv. sect. just in front of foramen Monroi; 45x. AZAN-MALLORY.

tically differentiated as an uninterrupted cortical layer passing from one side of the brain roof over to the opposite". In this primordial cortex the pyriform component differentiates somewhat earlier than the hippocampus. In the subsequent development a secondary delamination starts from the ventricular layer corresponding to a general pallium causing "a frontal separation of the hippocampal pallium from the pyriform lobe".

In Polypterus there exists according to Holmgren two layers of cells in the pallial formation. Outside the ventricular cells appears a layer "sparsely

distributed in the dense neuropil mass of pallium". This, however, does not constitute a distinct cortical lamina as in Protopterus and embryonic stages of Selachians. The ventricular layer is subdivided into a medial, a dorsal and a lateral area. The same holds true in Ganoids and Teleosts, the ventricular cells, however, in these forms having mostly migrated from this layer. "In Acipenser, Scaphirhynchus and Polyodon the cortical cells form a cell lamina with cortical arrangement throughout the whole pallium, with but few cells in the ventricular position" (HOLMGREN, 1922; p. 427). The migrated cells, however, do not constitute a single lamina with densely packed cells as in Protopterus. Instead there exist several rows of cells the one outside the other, somewhat similar to the migrated pallial cells in Osmerus which "sind schichtenweise (cortical) mit fast zellenfreien Zwischenräumen geordnet" (HOLMGREN 1920). The conditions in Amia and Acipenser are clearly shown in JOHNSTON's figures (1911 b).

The ontogenetic development of Protopterus shows that the pyriform part of the cortical lamina is the first to differentiate, analogous to the conditions in Selachians. In this group, the development of the primordial cortex is followed by a second delamination, representing a general pallium. At first sight nothing like this exists in the dipnoan pallial formation. Conditions exist, however, especially in embryonic stages of Epiceratodus, which seem to me to indicate that, though there is no general pallium component in the cortex, the underlying ventricular layer shows a tendency to start a secondary cortical migration.

Fig. 32 shows a transversal section through the caudal parts of the hemispheric primordium in a 34.5 mm larva of Epiceratodus. In this there exists an irregularily arranged layer of cells between the ventricular cells and the cortex (*g.p.c.*, fig. 32). There is a difference in size between the ventricular cells and the cortex, the latter being somewhat greater and paler in colour. This also applies to the intersected cells. I interpret this layer as a rudiment of a general pallium, which is situated beneath the meeting point of the hippocampal and pyriform elements in the primordial cortex. During the development, however, it sinks back into its matrix layer, but is represented in the adult brain by the external parts of the thickened area of the ventricular cell-layer. The ventricular cortical cells are very numerous in this part. HOLMGREN (1922) has pointed out that the "dorsally greatly thickened cell-layer bordering the ventricular ependymes dorsal to the ventricle" in Lepidosiren and Protopterus corresponds to the general pallium rudiment of Selachians.

Thus, there exists in fishes a pallium which consists of a ventricular layer of cells and a cortex. The latter develops out of two parts which have migrated after each other, the latter representing a general pallium. In embryonic stages of Selachians these conditions are distinctly developed according to HOLMGREN's investigations, confirmed by BÄCKSTRÖM (1924). In Ganoids and

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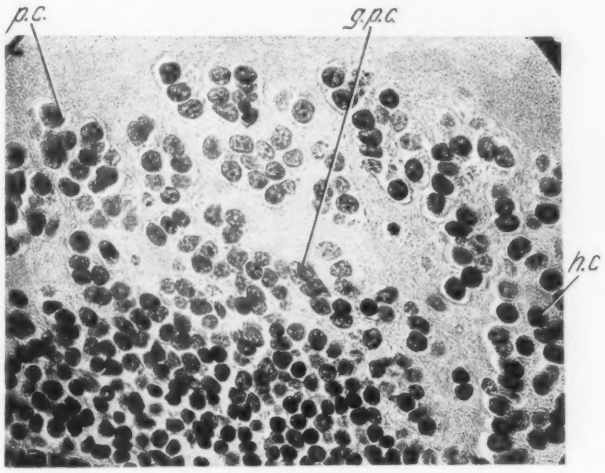

Fig. 32. *Epiceratodus Forsteri.* 34.5 mm. Transv. sect. through the pallial primordium; 112x. AZAN-MALLORY.

Teleosts the greater part of the ventricular cells have migrated out into the fibre layer, but the cortical arrangement of the migrated cells are often more or less obliterated.

In Dipnoans the reverse conditions exist in as much as the cortical migration has been exposed to a reduction. The general pallium component of the cortex merely shows a tendency to migrate out of its matrix layer. In the adult brain the cortex contains only hippocampal and pyriform parts, which are not separated from each other, i.e. it constitutes a primordial cortex. In connection with this reduction the boundaries of the ventricular layer have been obliterated. They are recognisable in Epiceratodus where in embryonic stages the cortex rudiment of the general pallium is also more conspicuous than in Protopterus.

In Chimaera a similar reduction seems to exist in the pallial formation, and, to judge from HOLMGREN's investigations, it must be more advanced in this form. For want of embryological material, however, it is impossible to interpret with full evidence the real nature of the pallial structure in Holocephalia.

From HERRICK's and SÖDERBERG's investigations especially it is evident that the Amphibians have a pallium subdivided into a primordium hippocampi, a lateral primordium pyriforme, and between them a primordial pars dorsalis pallii (HERRICK; 1927, 1933 a, b, c). The hippocampal formation is characterized by having a layer of scattered cells, external to the ventricular cells. There does not exist, however, any cortical structure in the amphibian pallium, but according to SÖDERBERG (1922) ontogenetic stages show a tendency to develop such a cortex. "The lack of differentiated cortices in telencephalon is probably a secondary manifestation, as we find in larvae, clearly separated from the inner ventricular layer a migrated cell-layer representing the cerebral cortex, which later is again forced in towards the ventricle. Thus the ventricular cell-layer in the adult Amphibia corresponds in general with the ventricular layer in the larvae as well as with their migrated cerebral cortex. The hippocampal pallium, however, forms an exception in this respect, its migrated

cortical parts being diffusedly spread over the corresponding portion of the ventricular wall" (p. 116). My own investigations on Hynobius and Necturus confirm SÖDERBERG's observations. Fig. 33 shows a transverse section through the pallial primordium of a 19.3 mm larva of Hynobius retardatus. Outside the ventricular cells there exists a relatively cell-free zone and outside this a typical cortical structure, which represents a rudiment of a primordial pallial cortex (*pall.c.*, fig. 33).

HERRICK (1922) questions the significance of cortical structures in embryonic stages of lower vertebrates. He is of the opinion, chiefly due to a very thorough and painstaking study of the fibre anatomical conditions, that there exists in the amphibian forebrain a pallium which contains primordia of the three principal pallial structures which undergo such a powerful development in higher vertebrates. According to HERRICK, cortical structures do not appear until the development of an extensive area, "somatic striatum", which develops due to the great increase in somatic sensory exteroceptive thalamic radiations correlated with the enlargement of the corpus striatum complex. This structure, which is quite free from direct olfactory and hypothalamic connections, does not appear in the vertebrate stem below reptiles (see HERRICK 1927, pp. 315—322).

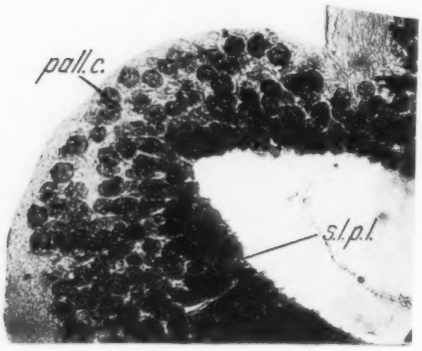

Fig. 33. *Hynobius retardatus*. 19.3 mm. Transv. sect. through the pallial primordium. 112x. AZAN-MALLORY.

As is clearly evident from HOLMGREN's investigations, cortical structures exist in other lower vertebrates in addition to the Dipnoans, and this fact, together with the occurrence of an embryonic cortical rudiment in Amphibia, seems to me to indicate that the group or groups from which the Amphibians originate ought to have had a pallial cortex. This cortex has been exposed to a reduction which may have started as early as in the amphibian ancestral group, and had there a structure similar to that which we now find in Dipnoans.

Fibre anatomy.

All parts of the pallium receive fibres from the tractus olfacto-dorsolateralis. Neurites from cortex and the ventricular layer assemble in the external fibre layer. In the most dorsal parts of the pallium they constitute caudally a rather well defined tractus cortico-habenularis (*Tr.c.h.*, fig. 29A—F). This tract runs immediately below the dorsal surface of the pallial formation, and in the telencephalon medium it is situated dorsally to the pars superior

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of nucleus preopticus (*Tr.c.h.*, fig. 29 E—F). Caudal to this nucleus it enters the stria medullaris complex and follows this up to the habenular commissure. In this it constitutes a commissura pallii posterior. The cortico-habenular tract is the most distinct of the pallial fibre connections.

From both the internal and external fibre layers fibres extend down ventrally and caudally, and they constitute in the caudal parts of the hemisphere the dorsal elements of the lateral forebrain bundle. This tractus cortico-tegmentalis contains most of the medullated pallial fibres, but with those are also a great number of unmedullated elements. This tract corresponds to the same tract found by HOLMGREN and VAN DER HORST in Epiceratodus.

In the caudal parts of the ridge of the anterior commissure there exist in Protopterus a number of crossing fibres, situated immediately dorsal to the most rostral parts of the pars inferior of the preoptic nucleus (*c.h.*, *n.pr.p.i.*, fig. 29 E, G). Reading the sections in a rostral direction, one will find that these commissural fibres turn upwards dorsally and rostrally, and that they are at first located medially to the lateral forebrain bundle. Somewhat more rostrally they are situated dorsally to this bundle. Following the sections in a rostral direction it is evident that these fibres continue up into the pallial fibre layers.

It is a typical feature of the hemispheres in Protopterus that the ventricular layer around the angulus dorsalis of the lateral ventricle almost reaches the hemispheric surface, and as a result of this, the pallial and septal fibre layers are almost separated from each other. In the rostral parts of the hemisphere there still exists a connection due to the extension downwards of fibres from the medial olfactory tract into the septal field. In a caudal direction this connection diminishes more and more and contains only horizontal fibres of the medial and dorso-lateral olfactory tracts. Investigations of preparations made by the Bielschowsky, Cajal, Bodian and Golgi methods show that, with the exception of a single fibre here and there, no direct fibre connections exist between the pallial and septal parts in the dorso-medial corner of the hemisphere. All these connections have to pass around the lateral and basal parts of the same. Similar conditions exist in Epiceratodus as a result of the development of the lingula interolfactoria which separates the medial pallial elements from the nervous part of the septal wall. Thus the connections of the hippocampal lobe with the corresponding structure in the opposite hemisphere do not pass through the medial wall, but are situated in the lateral wall. Those fibres which, as was stated above, cross in the caudal parts of the ridge of the anterior commissure and then run upwards in the lateral hemispheric wall to the pallium, thus constitute a pallial commissural connection, a commissura hippocampi. This has the same position among the anterior commissural fibres as the corresponding structure in Amphibians (*c.h.*, fig. 29 G). The rostral course of the fibres, however, is not the same, as they are located

in the lateral, not in the medial hemispheric wall. In this the dipnoan forebrain is similar to forms having exverted forebrains, i.e., the Polypterids, Ganoids and Teleosts.

A transverse section through the caudal half of the hemispheres shows the existence of two fibre systems in the basal parts, the one outside the other. The internal of these has longitudinal, the external transverse fibres (*v.f.b., d.B.*, fig. 29 A—C). The latter system constitutes a superficial tract which runs beneath the hemispheric surface in a dorsal direction, both in the lateral and the medial wall. In the latter it gives off fibres to the septum, and in the former to the lateral olfactory nucleus and the neighbouring parts of the pallial formation. This transverse fibre system constitutes an associational connection between the medial and lateral walls, and corresponds to a similar system in Amphibians, which, according to HERRICK, represents the d i a g o n a l b a n d o f B r o c a (see also p. 106).

HERRICK (1921 b) has shown the existence of an "olfactory projection tract" in Amphibians, which is homologous to the tractus pallii in fishes. In connection with the description of the lateral olfactory nucleus (p. 105) I have shown that a similar ascending hypothalamic fibre connection exists in Protopterus. The fibres of this tract, however, are very difficult to distinguish from those of the lateral forebrain bundle which they enter, but the preparations show that they follow this bundle in a rostral direction. They probably constitute a t r a c t u s p a l l i i, homologous to the same structure in other lower vertebrates. As a result of the scantiness of my Golgi-material, it is impossible to analyse with full evidence the great number of fibres which constitute the white matter of the pallial hemispheric wall. I have already (p. 81) pointed out the evident lack of myelinisated elements in the hemispheres of Protopterus. This adds to the difficulties of making a clear understanding of the different fibre elements of the forebrain. In connection with this I want to call attention to the investigation of KREHT (1940). In studying the fibre structures in the brains of different Anura and Urodela he points out that "Das Endhirn besitzt neben dem basalen Vorderhirnbündel nur bei einiger der von mir bearbeiteten Amphibien noch weitere allerdings schwach markhaltige Systeme" (p. 280).

NUCLEUS OLFACTORIUS LATERALIS.

Adult conditions.

This nucleus is situated in the lateral hemispheric wall, immediately ventral to the pallium. It is characterized by having a very thin ventricular layer (fig. 29 A—C). The most rostral parts are situated beneath the caudal parts of the olfactory bulb, and the nucleus extends in a caudal direction like a

broad band. It is a hemispheric structure along practically its entire extension, and in telencephalon medium it is replaced by the pars superior of nucleus preopticus (*n.olf.l.*, *n.pr.p.s.*, fig. 9 C). Ventrally to the nucleus olfactorius lateralis lies the tuberculum olfactorium. In the rostral parts of the hemisphere the boundary between these structures is indistinct. Caudally the "cortex olfactoria" of the tuberculum indicates the dorsal limit of this formation (fig. 29 B—D).

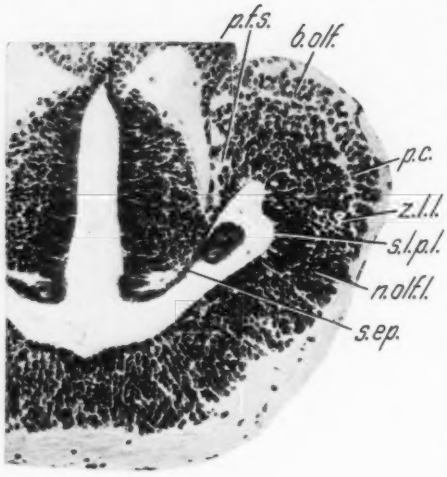
The lateral olfactory nucleus in Protopterus is subdivided into a pars dorsalis and a pars ventralis. The former constitutes a dorso-laterally extended cell-lamina, the medial part of which is in contact with the pars ventralis (*n.olf.l.p.d.*, *n.olf.l.p.v.*, fig. 29 A—C). It is easily distinguished from the pallial formation since the cell-nuclei are much paler in preparations stained with cresyl-violet. In Bielschowsky-preparations they are characterized by their greater size in comparison with the pallial cells.

Pars ventralis constitutes a thin ventricular band, ventrally to the basal parts of the pars dorsalis (*n.olf.l.p.v.*, fig. 29 A—B). In some parts this band is slightly thickened. Outside these thickened parts there exist a few scattered cells. The most caudal parts of the nucleus olfactorius lateralis are built up exclusively by pars ventralis, which is comparatively thick here (*n.olf.l.p.v.*, fig. 29 D).

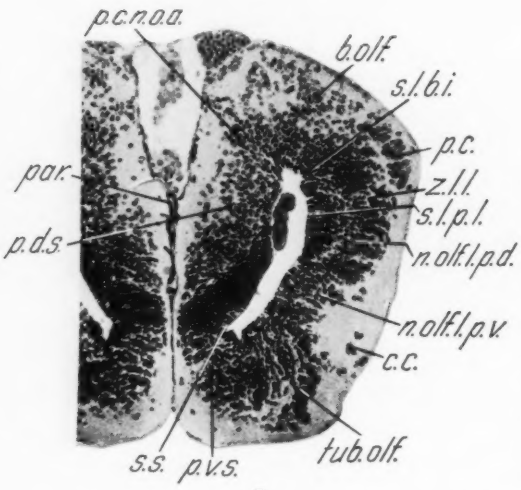
Golgi-preparations show that there is no structural difference between the cells in pars dorsalis and pars ventralis. They have a short principal dendrite with brush-like ramifications which reach out towards the hemispherical surface. In pars dorsalis some of these dendritical branches extend into the pallial fibre layers. The neurites contribute to the enormous fibre mass accumulated outside the lateral olfactory nucleus. They also build up a very well pronounced subependymal plexus in the pars ventralis.

Development.

The nucleus olfactorius lateralis differentiates rather late in the ontogenetic development, and in larvae between Stage 5 and 6 the lateral subpallial parts still constitute a thick ventricular layer of irregularly arranged cells, ventrally to the pallial primordium and the sulcus limitans pallii lateralis (*n.olf.l.*, fig. 34 A). There often appears an indistinct zona limitans lateralis in the border region between pallial and subpallial parts (*z.l.l.*, fig. 34 A). In a larva, somewhat older than Stage 6, there exists a dorsal and ventral cell condensation in the lateral subpallial wall. The ventral one begins to separate from the ventricular layer and constitutes the primordium of the tuberculum olfactorium cortex (*tub.olf.c.*, fig. 34 B). The dorsal part, pars dorsalis of the lateral olfactory nucleus (*n.olf.l.p.d.*, fig. 34 B), is separated from the tubercular condensation by an area in a ventricular position and characterized by less



A.



B.

Fig. 34 A—B. *Protopterus annectens*. A 20.2 mm, transv. sect. at the level of foramen Monroi; 67x. B 30 mm, transv. sect. somewhat in front of the same foramen; 60x. AZAN-MALLORY.

densely packed and more palely stained cell-nuclei. This is the pars ventralis of the nucleus olfactorius lateralis (*n.olf.l.p.v.*, fig. 34 B) and the three nuclear areas together constitute a curved cell-lamina. Pars dorsalis is easily distinguished from the heavily ependymated areas around the sulcus limitans pallii lateralis (*s.l.p.l.*, fig. 34 B), and there also exists an indistinct zona limitans lateralis dorsal to the nucleus (*z.l.l.*, fig. 34 B). During the subsequent development the changes are not great. The pars dorsalis becomes more pronounced and pars ventralis thinner (cf. fig. 29 C, 34 B).

Comparison.

HOLMGREN (1922) has shown that in embryonic stages of Selachians, the lateral olfactory nucleus appears as a cell-condensation dorsally to the tuberculum olfactorium. This condensation is located in the external parts of the relatively broad ventricular cell-layer. In an 80 mm larva of Acanthias it constitutes a "great cellular condensation with somewhat cortical aspect dorsal to the lateral border of the tuberculum olfactorium cortex".

According to HOLMGREN the nucleus olfactorius lateralis in Chimaera resembles very much the same structure in Selachians. It has a greater extension but in the former it also appears as a cell-condensation in the outer layers of the ventricular cells.

In Amia and Lepidosteus the nucleus is divided into two parts. "The nucleus olfactorius lateralis is composed of a lateral part, forming a cell-lamina in the lateral portion of the brain wall. From this lamina a process extends medially to join the ventricular ependymal layer just below the zona limitans, dorsal

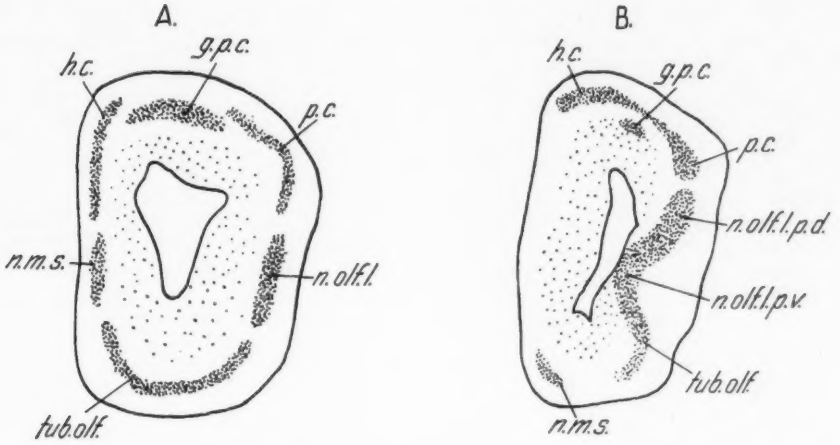


Fig. 35. Schematic drawing of transv. sect. through the embryonic hemisphere in Squalus (A) and Protopterus (B).

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to the precommissural body" (HOLMGREN 1922, p. 428). The latter according to HOLMGREN is homologous with the tuberculum olfactorium.

In Teleosts the lateral nucleus is situated in the basal subpallial parts in the vicinity of the forebrain surface (HOLMGREN, 1920). It is separated distinctly from the ventricular layer.

In lower vertebrates the structure of the nucleus olfactorius lateralis thus is somewhat different in the different groups. Either it appears as a more or less cortex-like structure in, or just outside, the outer layers of the ventricular cells, or it has migrated out in the fibre layer but does not have a cortical appearance. In this case it may be in contact with the ventricular layer (Ganoids) or completely separated from this (Teleosts). In Dipnoans the nucleus in question is situated ventricularily, but a part of it, pars dorsalis, has a more independent position and a somewhat cortical structure. The pars dorsalis and pars ventralis in Protopterus may correspond to the lateral and medial parts of the lateral olfactory nucleus in Ganoids. The ontogenetic development of this nucleus, however, seems to me to indicate a closer relationship to selachian conditions. In embryonic stages of the latter the tuberculum olfactorium cortex and nucleus olfactorius lateralis appear as an almost continous cell-lamina external to the ventricular cell-layer (HOLMGREN 1922, fig. 17 B). If the border region between these two structures were pushed up against the lateral ventricle, we should obtain exactly the same conditions as in the lateral hemispheric wall in Protopterus (fig. 35 B). The embryonic stages in Protopterus show such a ventrically directed pressure of the middle part of a cell-layer, which in its dorsal part is developing a pars dorsalis of the nucleus olfactorius lateralis, and in its ventral parts a cortex of tuberculum olfactorium (cf. figs 34 A, B;

35). This medially directed pressure is probably due to the powerful development of fiber masses belonging to the lateral forebrain bundle. This is situated laterally to the pars ventralis of the lateral olfactory nucleus and fills up an area bounded medially by the cell-layers of pars ventralis and dorsalis and the cortex of the tuberculum olfactorium (fig. 29 C).

In Epiceratodus this medially directed pushing inwards of the lateral olfactory nucleus seems to be more pronounced, as I have not been able to observe any distinctly differentiated pars dorsalis in the material at my disposal. Scattered cells, however, appear external to the ventral parts of the nucleus, as was the case in Protopterus. Do they perhaps indicate the extension of a former more laterally situated nucleus (see also p. 115). In connection with this I want to point out that the fibres belonging to the lateral forebrain bundle are not concentrated in a relatively small area as in Protopterus, but are accumulated outside to the entire dorso-ventral extension of the nucleus in question. These conditions may explain the difference in the structural appearance of nucleus olfactorius lateralis in Protopterus and Epiceratodus.

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GERLACH (1933) distinguishes in Protopterus a nucleus olfactorius lateralis ventrally to the sulcus limitans pallii lateralis. My pars dorsalis he seems to consider to be a pallial structure as he points out that the pallial cortex "an ihren ventrolateralen und dorsomedialen Grenze mit ihren matrix in Verbindung steht". Pars dorsalis ought thus to be a ventro-medial continuation of the pallial cortex. The ontogenetic development, however, shows that the pars dorsalis of the nucleus olfactorius lateralis develops out of the dorsal part of the arched cell-lamina situated ventrally to this sulcus. In Bielschowsky-preparations the cells of pars dorsalis are darkly stained, in marked contrast to the pale cells of the pallial cortex.

ELLIOT SMITH (1908) is of the opinion that the nucleus olfactorius lateralis in Lepidosiren constitutes a corpus striatum. HOLMGREN (1922) points out that "Really this part projects a little into the lateral ventricle as to suggest a striatum, but there are no special structures proving that it is really a striatum" (p. 419). Further HOLMGREN states that the olfactory nucleus probably corresponds to this nucleus and a "striatal swelling" in Selachians.

DART (1920) considers part of the lateral hemispheric wall to be a hypopallium, which in Lepidosiren is situated between the pallium and the tuberculum olfactorium. "It confirms to all known criteria of the region called hypopallium in reptilian forms for it lies between the above-stated regions and already shows a 'bending in' which has affected the contour of the ventricular wall". To me it does not seems probable that the "bending in" of the ventricular wall and cell-layers of Protopterus and Lepidosiren is a primordium of a hypopallial ridge, comparable to the same structure in reptiles. In this group the hypopallial formation causes a considerable thickening of the lateral hemispheric wall. This is not the case, however, in lungfishes.

The swelling of the ventricular wall corresponds to a bending in of the external lateral wall and as a result of this the lateral wall becomes slightly arched, not thickened (fig. 29 A—C). This is due to the powerful development of the tuberculum olfactorium which in Protopterus causes a swelling of the basal parts of the hemisphere. ELLIOT SMITH (1919) points out that the hypopallial structure is pallial in origin. Nucleus olfactorius lateralis (DART's hypopallium) develops out of subpallial parts.

HERRICK (1921 b) has made a close study of the ventro-lateral parts of the hemisphere in Amphibians. He states that in the frog a tractus olfacto-ventrolateralis originates in the acessory olfactory bulb and ends in an area situated caudally in the lateral hemispheric wall and at the level of the foramen Monroi. According to him this area constitutes a nucleus amygdalae. Immediately caudal to the olfactory bulb there exists an undifferentiated area which receives secondary olfactory fibres, and behind this there lies a "true corpus striatum". In Urodeles HERRICK finds a tractus olfacto-ventrolateralis coming from a rudimentary accessory bulb. This tract, however, also contains fibres from other parts of the bulbus olfactorius. In Urodeles there exists a nucleus ventro-lateralis "at the level of the interventricular foramen, less sharply defined than in the frog, contains a considerable collection of nerve cells and a dense neuropil related chiefly to the lateral forebrain bundle" (p. 243). This nucleus corresponds to both the nucleus amygdalae and the corpus striatum of the frog. It is the terminus of the ventro-lateral tract. It also receives ascending fibres from thalamus and is connected with the hypothalamus by means of an "olfactory projection tract" (tractus pallii in fishes). Unlike the conditions in Anurans secondary olfactory fibres reach "all parts of the lateral wall of the hemisphere, including the distribution area of the lateral forebrain bundle in the ventro-lateral quadrant. There is therefore neither a true striatum nor a true amygdala in the Urodeles, but a relatively undifferentiated area in the ventro-lateral quadrant which retains some of the characteristics of the lateral olfactory nucleus, which primitively occupied this region and at the time has acquired under the influence of its ascending non-olfactory connections the character of a common primordia of both the corpus striatum and amygdala" (p. 256). In Triton, SÖDERBERG (1922) observes a nucleus olfactorius lateralis and ventrally to this there exists an area which corresponds both to a corpus striatum and a tuberculum olfactorium.

Before making any comparison of the structure of the nucleus olfactorius lateralis in Dipnoans and Amphibians, I should like to give an account of the fibre connections of this nucleus as I have found them in Protopterus.

All parts of the nucleus olfactorius lateralis receive fibres from the tractus olfacto-ventrolateralis (p. 81), which leaves the bulbar formation in its most ventral and caudal parts. According to GERLACH (1933) these parts probably

correspond to an accessory olfactory bulb, but I have (RUDEBECK, 1944) pointed out elsewhere that this structure is probably to be found in the area containing the pallial supracortical cells. I have not been able to observe whether this structure sends any fibres down into the ventro-lateral olfactory tract as is the case in Amphibians.

Pars dorsalis and pars ventralis receive fibres from the medial and lateral component of this tract respectively (see also p. 81).

The fibre layer outside the lateral olfactory nucleus is dominated by the fibre mass belonging to the lateral forebrain bundle and it is rather difficult to make an analysis of this structure, but the facts given below show some of the principal points of the connections between the nucleus olfactorius lateralis and other parts of the brain.

In the anterior two thirds of this nucleus, fibres originate which run out laterally from the ventricular layer and then turn in a caudal direction. Together with the tractus olfacto-ventrolateralis they constitute a fibre unit medial to the lateral forebrain bundle. They are not made up of any distinct bundles. Caudally the fibres extend downwards into the dense mass situated inside the cortex of the tuberculum olfactorium. From this area they run medially to decussate in the anterior commissure (*Tr.olf.hyp.l.*, fig. 29 D). Caudal to this there exists a broad band of fibres outside the pars inferior of the preoptic nucleus (*Tr.olf.hyp.*[*l.+m.+v.*], fig. 29 F). This band contains fibres from the anterior parts of the septum and the tuberculum olfactorium. To these are added the fibres from the anterior part of the lateral olfactory nucleus which constitute a tractus olfacto-hypothalamicus lateralis (*Tr.olf.hyp.l.*, fig. 29 B—D).

In the caudal parts of the nucleus there exists a powerfully developed subependymal plexus, which opens ventrally into the fibre layer between the cortex and the ventricular cells of pars posterior of tuberculum olfactorium. This plexus gives rise to at least two different tracts. Some of the fibres gather into rather distinct bundles which break through the ventricular layer of the pars ventralis, and at the level of the foramen Monroi enter the dorsal parts of the lateral forebrain bundle. Some of these fibres mingle with the elements of the cortico-tegmental tract. Such fibres have been observed by HOLMGREN and VAN DER HORST in Epiceratodus, but, owing to the material at their disposal, they had no opportunity to decide the nature of these fibres. In a Bielschowsky-preparation I have been able to follow such a bundle from the subependymal plexus of the nucleus olfactorius lateralis. At the level of the optic chiasma it is situated most dorsally in the lateral forebrain bundle. Somewhat caudally to this point it begins to disintegrate and at the level of the tuberculum posterius the fibres are lost among the other elements. Sagittal sections of Bodian-preparations show that these dorsal components of the

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lateral forebrain bundle enter the basal parts of the mesencephalon. In Amblystoma (1927) and Necturus (1933 a) HERRICK describes well developed connections between the caudal parts of the nucleus olfactorius lateralis and the tegmentum and the interpeduncular nucleus. As in these forms there also exists in Protopterus a tractus strio-tegmentalis (*Tr.str.t.*, fig. 29 B, D).

The fibres which extend downwards from the subependymal plexus in the lateral olfactory nucleus into the fibre layer internal to the cortex of tuberculum olfactorium, assemble in this layer (*Tr.str.hyp.*, fig 29 C), and then some of them cross in the anterior commissure. Caudal to this both crossed and uncrossed fibres of this tract mingle with elements belonging to the

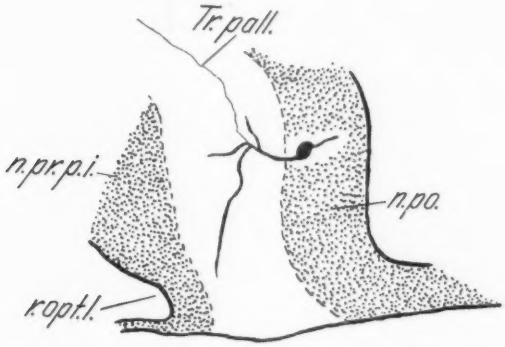

Fig. 36. *Protopterus annectens.* Adult. Cell in nucleus postopticus. GOLGI.

olfacto-hypothalamic systems and follow these to the hypothalamus. This tract corresponds to the tractus strio-hypothalamicus of HOLMGREN and VAN DER HORST (*Tr.str.hyp.*, fig. 29 C—E).

Because of the existence of tractus olfacto-hypothalamicus lateralis and tractus strio-hypothalamicus, the connections between the lateral olfactory nucleus and the hypothalamus are well pronounced. This is further increased by an ascending tract from the anterior parts of the hypothalamus. In this part (nucleus postopticus) the cell-bodies are characterized by having a ventriclewards directed offshoot (fig. 36). Opposite to this a powerful dendrite leaves the cell and branches out inside the postoptic commissure. The neurite starts from the dendrite and turns dorsally and rostrally to join the lateral forebrain bundle.

HERRICK (1921 b) describes in Amblystoma a nucleus in the anterior parts of the hypothalamus, which gives rise to the olfactory projection tract (tractus pallii). "The neurones of this nucleus are of the same peculiar form as those which border the infundibulum farther ventrally and posteriorly. Each is connected with the ventricular surface by a thick process which may join

the cellbody or the base of the principal dendrite . . . . . The rough and slightly thorny dendrites spread widely forward and lateralward among the terminals of the descending fibres of the projection tract, the medial forebrain bundle and the most caudoventral component of the post-optic commissure, the tractus thalamo-hypothalamicus cruciatus" (p. 248).

The cellular structure in the nucleus which gives rise to the olfactory projection tract in Urodeles corresponds very well to the same conditions in the anterior part of the hypothalamus in Protopterus, and I am of the opinion that the neurites originating in this nucleus constitute a tractus homologous to the olfactory projection tract of Urodeles. In this group the tract joins the lateral forebrain bundle and, while easily distinguished from it, follows it rostrally. In Protopterus the fibres do not constitute bundles, but after turning in a rostral direction mingle with the fibre elements of the lateral bundle. The caudal parts of the nucleus olfactorius lateralis receive terminal branches from rostrally running fibres belonging to the lateral forebrain bundle complex, a fact which is evident from Golgi-preparations. In all probability some of them belong to the olfactory projection tract (tractus pallii, see also p. 98). There is a possibility that some of these end branches belong to ascending thalamic radiations, but I have not been able to find any real evidence to support this theory.

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Pars superior of nucleus preopticus sends a tractus preoptico-habenularis to ganglion habenulae, and this tract also contains fibre elements from the neighbouring parts of the lateral olfactory nucleus (see further p. 132).

I have shown earlier in this work (p. 97) that the connections between the lateral and medial wall are to be found in the basal transversal fibre tract, corresponding to a diagonal band of Broca. This contains association fibres between the septum and the nucleus olfactorius lateralis.

The caudal parts of this latter nucleus (and the neighbouring parts of tuberculum olfactorium) constitute in Protopterus an important center of correlation, which is evident, i.e., from the accumulation of endbranches from tractus olfacto-ventrolateralis and hypothalamic connections (olfactory projection tract). Pallial fibres also extend down into this neuropilar mass, together with association fibres from the medial hemispheric wall. This powerful neuropil corresponds to a similar structure in the caudal parts of the ventro-lateral quadrant in the telencephalon in Amblystoma and Necturus (HERRICK, 1927, 1933 a).

HERRICK (1921 b) has made a summary of the results of his investigations on the structure of the lateral hemispheric wall in urodeles (confirmed by his later studies; 1933 a). In the following table I have made a comparison between some of HERRICK's results and those found in my own investigations on the lateral olfactory nucleus in Protopterus.

Comparison between the nucleus olfactorius lateralis in Protopterus and the correspondent structure in Urodeles.

Urodeles (HERRICK, 1921)	Protopterus (The author)
The lateral wall of the hemisphere is thin and undifferentiated except for a thickened region laterally of the interventricular foramen, here termed the ventrolateral nucleus of the hemisphere.	The ventricular part of the lateral olfactory nucleus, pars ventralis, is thin and undifferentiated except for its caudal parts laterally to foramen Monroi, which are thickened.
The relations of the ventrolateral area to the ascending and descending fibres of the lateral forebrain bundle indicate that here is to be sought the functional equivalent of the corpus striatum (paleostriatum); but since there is no group of neurons related with the thalamic and tegmental fibre systems of the lateral forebrain bundle which do not also receive secondary olfactory fibres (by the ventrolateral olfactory tract), or ascending hypothalamic fibres (by the olfactory projection tract), or both of these systems, it is clear that in the urodele there is no anatomical structure to which the name corpus striatum can properly be given.	The caudal parts of the nucleus olfactorius lateralis are related to tegmentum and possibly also to thalamus. These parts are influenced by the tractus olfacto-ventrolateralis, and have hypothalamic connections by the ascending olfactory projection tract. As there is no part of the lateral olfactory nucleus influenced by ascending components of the lateral forebrain bundle which do not receive secondary olfactory fibres, there is no part which can be identified as a true corpus striatum.
The amygdaloid complex of reptiles is related to the lateral olfactory tract, the hypothalamic olfactory projection tract, the stria medullaris for the habenula, the stria terminalis, and the diagonal band of Broca. The first three of these fibre tracts (and probably the other two) are related with the ventrolateral nucleus of the urodele hemisphere, but not with any specific group of neurons within this nucleus. Here then is the physiological primordium of the amygdala, but this nucleus as a morphological entity has not emerged from the common olfacto-striatal matrix.	The caudal parts of the nucleus olfactorius lateralis are related to the ventrolateral olfactory tract, the hypothalamic olfactory projection tract, to tegmentum, to septum by means of the diagonal band of Broca and to the habenula by the tractus preoptico-habenularis. Judging from its fibre connection these parts correspond to the ventrolateral nucleus of the urodeles.

The comparisons show that there exists in the lateral hemispheric wall, ventrally to the sulcus limitans pallii lateralis, an area which in Dipnoans and Urodeles is related to the tractus olfacto-ventrolateralis. The caudal parts of this nucleus olfactorius lateralis constitute in Urodeles a primordium of a corpus striatum and a nucleus amygdala. This primordium is connected to tegmentum, thalamus, hypothalamus, ganglion habenulae to which are added association fibres from pallium and septum. The same connections also exist in the caudal parts of the lateral olfactory nucleus in Protopterus (the thalamic

connection is uncertain). As a result of this, these parts are at least homologous to the nucleus ventrolateralis of the Urodeles, and may contain a primordium of a corpus striatum. I will take up this discussion further on in connection with the description of the pars superior of the preoptic nucleus (p. 132).

TUBERCULUM OLFACTORIUM.

Adult conditions.

The basal parts of the hemispheres in Dipnoans are extremely well developed compared to other lower vertebrates, and constitute "a large horizontally placed sausage-shaped bag" (ELLIOT SMITH, 1908). The ventral and lateral parts of this bag contain the tuberculum olfactorium, which is characterized in Protopterus and Lepidosiren by having a well differentiated cortex in its caudal parts. A closer study of the cellular arrangement of tuberculum olfactorium shows a gradual change from a relatively undifferentiated structure in the rostral parts of the brain to the powerfully developed cortical structure, which in the ventro-lateral parts of the external, caudal hemispheric wall is indicated by the ventro-caudal lobe (*v.c.l.*, figs 9 A; 29 D—F).

In the parts of the tuberculum olfactorium which are situated ventrally to the olfactory bulb, there exists a well developed, ventricular cell-layer containing a subependymal plexus. In the external parts of this layer the cells are more scattered and in the medial and ventro-medial parts especially they almost reach the hemispheric surface. In sections stained with cresyl-violet the cell-nuclei are somewhat paler and larger than in the ventricular cells. This cellular arrangement is a characteristic feature of the anterior half of the tuberculum olfactorium. Caudally to this there begin to appear isolated cells or cell-clusters in the fibre layer external to the lateral and ventro-lateral parts of the ventricular layer (*c.c.*, fig. 29 A—B). The ventro-medial scattered cells now show a tendency to arrange themselves in a somewhat cortex-like structure (*v.m.c.*, fig. 29 A—B). The plexus subependymalis becomes more pronounced in a caudal direction and in the lateral parts of the tuberculum this plexus has separated distinctly the ventricular cells from the ependym. These cells now constitute a cortical structure which is connected dorsally with the pars ventralis of nucleus olfactorius lateralis (fig. 29 C). The cortex-like structure of the ventro-medial cells becomes more accentuated and they now are continued ventrally and ventro-laterally by the above mentioned lateral part of the tubercular cortex. The ventricular cells inside this ventro-medial part of the cortex become restricted in a caudal direction to a small area around the angulus ventralis and its caudal continuation caudal to the foramen Monroi (fig. 29 C—D).

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In tuberculum olfactorium, therefore, it is possible to distinguish a pars anterior, characterized by having cells arranged in a ventricular layer, and a pars posterior with a ventricular cell-layer and external to this a cortex and isolated cells and cell-clusters. There is no sharp boundary between these two parts as pars anterior gradually acquires the characteristics of the pars posterior.

The above mentioned cell-clusters constitute a very typical structure in the forebrain of Protopterus. I have found them in all my specimens of this animal, and according to ELLIOT SMITH's figures they also appear in Lepidosiren, where they seem to hold the same position. As is evident from a graphic reconstruction of the migrated cell-elements in the ventral and caudal parts of the hemisphere in Protopterus (fig. 9 C—D), these structures are situated externally to the anterior parts of cortex of tuberculum olfactorium (*cc.*, *tub.olf.c.*, fig. 9 C—D).

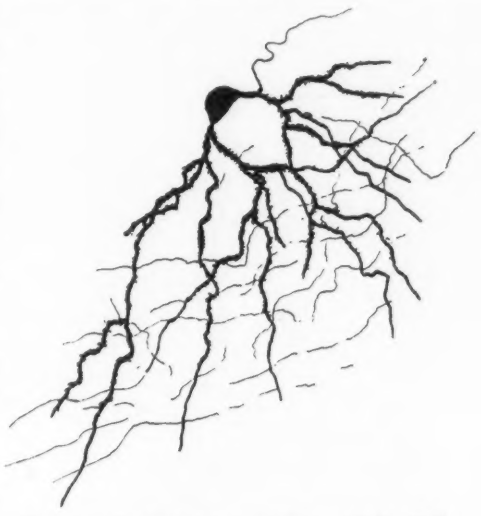

Fig. 37. *Protopterus annectens.* Adult. Cell from tuberculum olfactorium pars anterior; 200x. GOLGI.

The ventricular cells in the tuberculum have a short principal dendrite which branches off in a system of rather thin, slightly thorny dendrites. The neurite originates in the cell-body or in the principal dendrite, and runs into the fibre layer external to the ventricular cells or into the subependymal plexus. The scattered cells in the external layers of pars anterior and the ventromedial cells usually have two principal dendrites with fairly wide-spread richly developed system of thorny dendritical branches (fig. 37). This type of cells also builds up the cortex and the cell-clusters, in which, however, the dendritical branches are not so many but longer and often smooth. The neurites run into the external parts of the fibre layers of tuberculum.

Development.

As has already been stated (p. 99), the differentiation of the subpallial parts begins very late in the ontogenetic development. In Stage 5, however, it is possible to distinguish a cellular condensation in the ventrolateral parts of the hemispheric primordium (*tub.olf.c.*, fig. 38). In the external parts of this condensation there appear small clusters of cells

which lie partly in the fibre layer (*c.c.*, fig. 38). During the development fibres begin to appear internal to the most ventral part of the above-mentioned cell-condensation, which thus acquires a true cortex-like appearance (*tub.olf.*, fig. 34 B). Its dorsal part is, however, still connected to the ventricular layer and its dorsal continuation, pars ventralis of nucleus olfactorius lateralis (*n.olf.l.p.v.*, fig. 34 B). At the same time the fibre layer outside the primordium of the tubercular cortex has considerably increased and now, unlike Stage 5, separates distinctly this cortex from the hemispheric surface (cf. figs 38; 34 B). The cell-clusters, however, are now distinctly separated from the cortex, and are situated in the outer parts of the fibre layer (*c.c.*, fig. 34 B). Originally they belonged to the cortical primordium, but have been separated from this in the same manner as we are already familiar with from the development of the interglomerular cells in the olfactory bulb and the supra-cortical elements of pallium. During the development subsequent to the stage shown in fig. 34 B, the subependymal fibres begin to appear inside the part of the ventricular cells which contains the cortical condensation, and finally separate this part from the ependymal cells. Only its most dorsal part is still in contact with the pars ventralis of nucleus olfactorius lateralis.

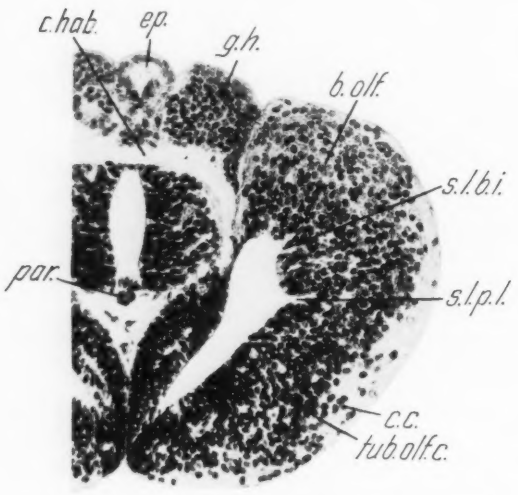

Fig. 38. *Protopterus annectens.* 15 mm; transv. sect. just in front of foramen Monroi; 75x. AZAN-MALLORY.

In embryonic stages the tuberculum olfactorium is exclusively a laterally and ventro-laterally situated structure, but due to the deepening of the hemispheres, which starts in the tubercular primordium, this structure in the adult brain also builds up the ventro-medial part of the hemisphere.

Comparison.

ELLIOT SMITH (1908) has studied the tuberculum olfactorium in Lepidosiren, and judging from his description and figures of this brainpart there is no structural difference between this species and Protopterus. He points out that he is not sure about the relationship between tuberculum and corpus

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striatum, "there is no certain criterion to enable a distinction to be drawn between corpus striatum and the tuberculum olfactorium" (p. 531).

I have pointed out above (p. 107) that we have to look for what corresponds to a primordium of a corpus striatum in the caudal parts of the nucleus olfactorius lateralis in Protopterus, that is dorsally to the pars posterior of tuberculum olfactorium. ELLIOT SMITH also states that "during the process of pushing out the great tubercular sac, the corpus striatum may have been relegated chiefly to the lateral wall and the tuberculum olfactorium to the ventral and mesial walls of the vesicle" (p. 531). ELLIOT SMITH's corpus striatum seems to correspond to the entire lateral olfactory nucleus, not only to its caudal parts.

GERLACH (1933) is of the opinion that the difference existing between the anterior and posterior parts of the tuberculum olfactorium in Protopterus, reflects the ontogenetic development of the cortex. In the anterior part the ventricular cell-layer begins to loosen in its external parts, and there follows from this a layer of scattered cells. Reading the sections in a caudal direction one finds cell-islets, distinctly separated from the ventricular layer. "Diese werden zahlreicher, verschmelzen miteinander, und schliesslich liegt das Bild der voll ausgeprägten Rinde vor" (p. 327).

An investigation of the cortex of tuberculum olfactorium in embryonic stages and the adult brain shows, however, that this cortex is a rather complex structure. It is possible to distinguish three different parts; 1) the ventral and ventro-medial lamina (*v.m.c.*, fig. 29 A—B) which, reading the sections in a rostral direction dissolves, and in the anterior part of the tuberculum is representated by the scattered cells outside the ventricular layer in the medial and ventro-medial parts; 2) the lateral lamina which in the adult brain consists of the entire ventricular cell-layer, which in this part has been pushed in a lateral direction as a result of the powerful accumulation of subependymal fibres between this layer and the ependymal cells (*tub.olf.c.*, fig. 29 C); 3) the isolated cell-clusters external to the anterior parts of the cortex. The ontogenetic development shows that these parts probably contain two structures. The differentiation of the cortex starts here with a cell-condensation in the outer layer of the ventricular cells. Later on these cells together with the cell-condensation are separated from the ependymal cells by the subependymal plexus. In the adult brain it is not possible to distinguish this cell-condensation from the originally ventricular cells. The ontogenetic development also shows that the cell-clusters develop out of the above mentioned cell-condensation, but later become separated from this structure. These conditions seems to me to indicate the existence of an earlier, more laterally situated cortical lamina, representated in the present species of dipneumonian dipnoans by a remnant in the shape of the isolated cell-clusters, and in embryonic stages further indicated by the cell-condensation

in the matrix layer. The development, however, does not indicate that the present cortex has developed as a result of a gathering of the above mentioned cell-clusters — an opinion asserted by GERLACH.

According to HOLMGREN and VAN DER HORST, tuberculum olfactorium in Epiceratodus consists of a pars anterior and a pars posterior. The former has a relatively thick ventricular layer (stratum gangliosum internum), in the external parts of which there exists a layer of larger cells (stratum gangliosum externum). This structure corresponds to the pars anterior in Protopterus. In the ependym of pars posterior there exists a "great number of short grooves or pits. With these correspond clusters or masses of cells projecting from the ventricular layer into the neuropil substance of the tuberculum (str. medullare) as to make one suggest that the pits once acted as centre for the proliferation of the cells of the clusters, referred to above. These pits are restricted to the tuberculum olfactorium alone. Thus in this brainpart of Ceratodus no distinct cortical arrangement is present as in Protopterus and Lepidosiren" (p. 73).

A comparison between the adult brains of Epiceratodus and Protopterus shows that in the former species the hemispheric wall is of a uniform thickness throughout (except in the dorsal, epithelial part of the medial wall). In the latter, however, the basal parts of the hemispheric wall, around the angulus ventralis of the lateral ventricle, is much thicker than in other parts. In these thickened parts there exists a large number of small, closed ependymated cavities (fig. 39 A). These always appear ventrally to the lateral ventricle in the pars posterior (fig. 39 B), and are more numerous in its caudal parts. The fact that these cavities are lined by an ependymal tissue seems to indicate that they are remnants of a ventral continuation of the lateral ventricle. The conditions in Epiceratodus also seem to support this view. The ventral parts of the very much deeper lateral ventricle in this species may correspond to such a ventral diverticle existing formerly in Protopterus, and the above mentioned closed cavities then would correspond to the short grooves and pits in the ependymal lining of the pars posterior in Epiceratodus.

In connection with this I should mention that JOHNSTON (1915) has shown the existence of somewhat similar structures in a Chelonian (Cistudo carolina). He found "a peculiar vesicular structure" forming cell-clusters which contain a cavity. "The greater number of these structures are found around the depression of the ventricle which extends down into the tuberculum but some are found also in the lateral part of the caudate not far from the middle ventricular groove" (p. 402). JOHNSTON is of the opinion that these cell-clusters do not contain neurons, as he has not been able to show the existence of any fibres belonging to these cells. "I suspect that these vesicles are composed chiefly of ependymal cells and that their lumina represents vestiges of ventricular cavity which have been pinched off during development" (p. 403).

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JOHNSTON points out, however, that real neurons "are often found closely related to or imbedded in the ependym". Similar conditions exists in Protopterus as there often exists a gathering of neurons around the vesicular rudiments (fig. 39 A), conditions which, according to HOLMGREN and VAN DER HORST, also are valid for the short grooves and pits in the basal parts of the lateral ventricle in Epiceratodus.

The investigations of older embryonic stages of Urodeles will show that in Triturus, Hynobius, and Necturus for instance, we have the same arched cell-lamina in the lateral hemispheric wall as we have already observed in Protopterus, and which contains dorsally the primordium of nucleus olfactorius lateralis, and ventrally the tuberculum olfactorium. In Urodeles also there

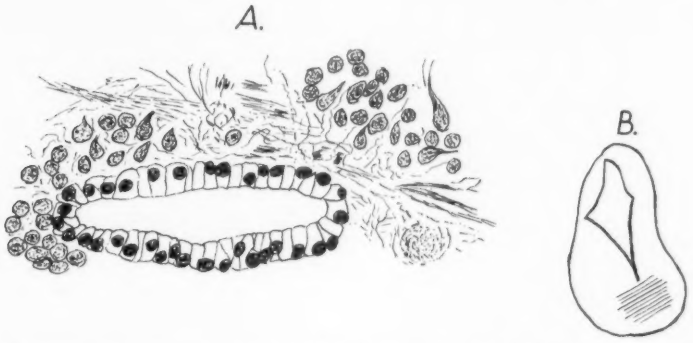

Fig. 39. *Protopterus annectens.* Adult. An ependymated vesicle from the pars posterior of tuberculum olfactorium in B indicated by the obliquely lined area. A 200x. BIELSCHOWSKY.

is a tendency to separate the tubercular primordium from the ependymal layer (fig. 40 B). No cortical structure appears in the adult animal, a condition common to the Urodela and the Epiceratodus.

Beneath the pallial parts, the ventricular layer in the lateral wall in an older larva of this species appears as a uniform layer with a somewhat indistinct cellular condensation in its dorsal parts, corresponding to a primordium of a lateral olfactory nucleus (*n.olf.l.*, fig. 40 A). In the ventral parts, around the angulus ventralis, the ventricular layer is thickened, and external to this there exists a very thin row of scattered cells with a somewhat cortical aspect (*tub.olf.c.*, fig. 40 A). During the development, however, this very rudimentary cortex disappears. The thickened part in the ventricular layer in larval Epiceratodus (primordium of tuberculum olfactorium) reminds one very much of the thickened part of the ventricular layer in the ventral parts of the lateral wall in Triturus (*tub.olf.*, fig. 40 B). In both species it is situated outside a powerfully ependymated groove (*a.v.*, fig. 40 A—B), which during the development constitutes the angulus ventralis of the lateral ventricle. In Urodela, however, I have not been able to find any structures which could be compared

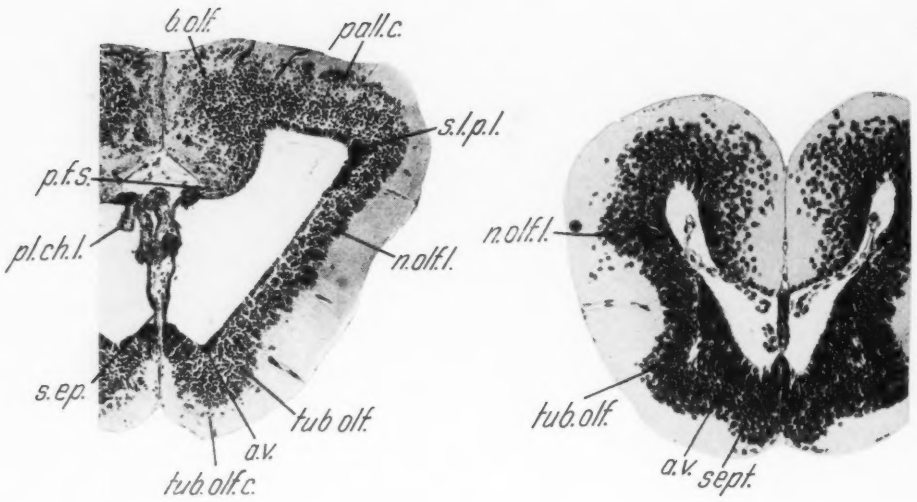

Fig. 40 A—B. A *Epiceratodus Forsteri*, 43.5 mm; transv. sect. at the level of the septum ependymale; 45x. B *Triturus vulgaris*, 21 mm; transv. sect. immediately in front of foramen Monroi; 75x. AZAN-MALLORY.

with the rudimentary, embryonic cortex of the tuberculum in Epiceratodus. There is, however, a great resemblance between the structure of the embryonic lateral wall in Urodeles and the same parts in Protopterus (the arched structure of the common primordium of nucleus olfactorius lateralis and tuberculum olfactorium, the appearance of cell-free spaces between the tuberculum and the ependym). The existence of a rudimentary cortex in Epiceratodus and the conditions in Protopterus (see p. 111) indicate a reduction of an earlier, more pronounced cortex outside the tuberculum olfactorium, a reduction which may have gone much farther in the amphibian line of development.

In Selachians there exists a well developed cortex. In Ganoids and Teleosts the tuberculum olfactorium (pars superior of the precommissural body) maintains its ventricular position, and does not gives rise to any cortical structures (HOLMGREN, 1922). An investigation of older embryonic stages of Lepidosteus, however, shows that there exists a diffuse layer of cells external to the ventricular cells and separated from these by means of a cell-free zone. In some parts of this outer layer there appear cellular condensations, and it is connected dorsally to the lateral olfactory nucleus, reminding one of the conditions in older embryonic stages of Selachians. These conditions have previously been pointed out by JOHNSTON (1911 b).

In lower vertebrates with evaginated hemispheres, except in Epiceratodus and Amphibia, there exists a cortical structure outside the tuberculum olfactorium. The conditions in Epiceratodus, however, must be a secondary manifestation

due to a reduction, as the ontogenetic development indicates the earlier existence of such a cortex. Concerning the Amphibians, SÖDERBERG (1922) points out that in Anura the tuberculum olfactorium is better developed than in the Urodela, and in certain forms this structure may have an almost cortical appearance. KUHLENBECK (1922 b) has shown the presence of a well developed cortex of the tuberculum olfactorium in Gymnophiones. As it is also possible to show the existence of migrated cells outside the tubercular structure in ganoids (Lepidosteus), one has every reason to support HOLMGREN's statement that "It is, however, possible that the ventricular position is secondary in ganoids and teleosts, as well as in dipnoans and Amphibia" (HOLMGREN, 1922).

Fibre anatomy.

In Protopterus the fibre connections of the medial and lateral hemispheric walls are collected chiefly in the medial and lateral forebrain bundles. The fibre connections of the basal parts are also arranged in a distinct system of fibres, the ventral forebrain bundle[1]. This is situated ventrally to the cell-layers of pars anterior of the tuberculum olfactorium, and constitutes a broad fibre mantle consisting of longitudinal fibres (*v.f.b.*, fig. 29 A—D). Outside pars posterior it separates into an internal and an external layer on each side of the tubercular cortex. From both these layers fibres cross in the anterior commissure, and run partly to the hypothalamus, and partly to the basal parts of the opposite hemisphere. Such commissural fibres also exist between other secondary olfactory centres (septum, p. 127) and DART (1920) proposes a common name for these connections, commissura olfactoria. In Protopterus, however, this name would include fibre elements from quite a number of different telencephalic centres, and I prefer to indicate these fibres according to the centres they connect. The commissural fibres between the basal parts of the two hemispheres should thus constitute a commissura tuberculi olfactorii. The fibres originating in tuberculum olfactorium and by means of the ventral forebrain bundle connecting this structure to the hypothalamus, constitute a ventral parallel to the tractus olfacto-hypothalamicus lateralis from the nucleus olfactorius lateralis, that is, a tractus olfacto-hypothalamicus ventralis (*Tr.olf.hyp.v.*, fig. 29 D—F). Like the lateral tract this contains both crossed and uncrossed fibres.

HERRICK (1927, 1933 a) distinguishes immediately behind the olfactory bulb in Amblystoma and Necturus an area with "relatively unspecialized gray surrounding the bulbar formation". This nucleus olfactorius anterior, is

[1] In Urodeles the medial and lateral bundles have sometimes a common name, the basal forebrain bundle (HERRICK, 1933 a). In Protopterus the medial and lateral components are separated distinctly from each other by a powerful basal fibre system, for which reason it seems to be convenient to indicate the latter as the ventral forebrain bundle.

according to HERRICK subdivided into dorsal, lateral, medial and ventral parts and the two last correspond to "the tuberculum olfactorium of Mammals, a comparison which is strengthened by its contact with the caudate nucleus and by its fibre connections". In Mammalia there exists a tractus olfacto-habenularis anterior connecting tuberculum olfactorium with the habenular ganglion. "The corresponding tract of Amblystoma arises chiefly from the medial part of the anterior olfactory nucleus, with additions from the septal nuclei and adjacent regions including the ventral part of the anterior nucleus" (HERRICK, 1927; p. 290).

In the lateral parts of the external portion of the ventral forebrain bundle fibres collect, which break through the cortical lamina caudally at the level of the anterior commissure, and turns upwards in a dorsal direction, finally entering the ganglion habenulae. This t r a c t u s o l f a c t o - h a b e n u l a r i s v e n t r a l i s (*Tr.olf.h.v.*, fig. 29 D—E) contains fibres from pars anterior and pars posterior of the tuberculum olfactorium and corresponds, at least in regard to the fibres from pars anterior, to HERRICK's tractus olfacto-habenularis anterior in Urodeles.

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Nucleus taeniae.

The bulk of the fibres from the tubercular cortex joins the tractus olfacto-habenularis ventralis or the hypothalamic connections. The most caudal parts of the cortex give rise to a distinct but rather small tractus, which runs almost straight in a dorsal direction to join the stria medullaris complex. This habenular connection, originating in the most caudal part of the tubercular cortex, corresponds to the t r a c t u s t a e n i a e (*Tr.t.*, fig. 29 F) of Epiceratodus (HOLMGREN and VAN DER HORST). HOLMGREN has pointed out earlier (1922) that the caudal parts of the tuberculum olfactorium in Protopterus represent a nucleus taeniae. In Epiceratodus this structure consists of "some groups of cells clearly detached from the tuberculum olfactorium, which perhaps represent a nucleus taeniae" (HOLMGREN, VAN DER HORST). These cells are situated just at the level of the anterior commissure. GERLACH (1933) denies the existence of such a nucleus in Protopterus, and he points out that as KAPPERS has given the name nucleus taeniae to a structure which is the same as the tubercular cortex "scheint mir die Bezeichnung Nucleus taenie entbehrlich, zumal das kaudale Ende der Rinde in keiner Weise von den rostralen Anteilen abzugrenzen ist" (p. 367). In embryonic stages of Selachians, however, there is a cell-condensation situated "at the medial end of the olfactory cortices" (HOLMGREN, 1922) and this formation "that accompanies and immigrates from the inner part of the tuberculum olfactorium in Cajal preparations has been found to give rise to taenia fibres. It is the nucleus taeniae, hitherto not clearly demonstrated in selachians" (HOLMGREN 1922, p. 409). Even though

the area which gives rise in Protopterus to habenular fibres, distinctly separated from the ventral olfacto-habenular tract, constitutes a caudal continuation of the tubercular cortex, the very existence of these taenia fibres indicates that the area in question is a nucleus taeniae (*n.t.*, fig. 29 E). Its rostral connection with the tubercular cortex is not evidence enough to question the morphological significance of this nucleus.

BERGQUIST (1932) states that in Polypterus, Ganoids and Teleosts, there develops out of pars frontalis thalami a nucleus ventralis thalami mihi, which consists of "ventriculär liegenden prolifierten Zellen. Die letzteren bilden oft ein Zellensäule die in gleicher Richtung wie die Körperachse verläuft und parallel mit ähnlichen Zellensäulen im Nucleus medialis thalami und dorsalis thalami mihi liegt" (p. 255). According to BERGQUIST there do not exist corresponding structures in Epiceratodus and Amphibia. He remarks, however, that in the frog "sind ausgewanderte Zellen vorhanden" and the same holds true of a 17.5 mm larva of Protopterus.

The ontogenetic development shows that in older stages of Protopterus and Epiceratodus there exists an area of migrated cells external to the pars frontalis thalami in these species (*n.v.th.*, figs 6 G, 7 D, 8 C, G; 13 C, G). Rostrally this structure merges with the caudal parts of the pars superior of nucleus preopticus (*n.v.th.*, fig. 44). This corresponds to BERGQUIST's nucleus ventralis thalami.

The latter author has observed another migrated nucleus which he considers to be a nucleus taeniae. This is distinctly developed in Polypterus, Ganoids and Teleosts, that is, in the same forms which have a distinct nucleus ventralis thalami. BERGQUIST's Nucleus taeniae has "bei allen diesen Fischen während der Ontogenese Zellen sowohl aus der Pars praeoptica des Telencephalon als auch solche aus der Pars frontalis thalami des Zwischenhirns empfangen" (p. 255). As is evident from BERGQUIST's investigation, the nucleus in question, in larval stages of Ganoids and Teleosts, constitutes a rostral continuation of the nucleus ventralis thalami, and is situated externally to the nucleus preopticus. In trying to establish such a structure in Dipnoans we have to search in the caudal parts of the pars superior of the nucleus preopticus, as the rostral parts of the nucleus ventralis thalami in Dipnoans passes over into this structure. There does not exist, however, any differentiated part of the pars superior which can be said to be homologous to BERGQUIST's nucleus taeniae. KAPPERS indicated with this nucleus the cortex of the tuberculum olfactorium. He points out that the "basale Oberfläche der Pars striatalis" in Selachians corresponds to JOHNSTON's (1911 b) "area superficialis basalis", that is the cortex of tuberculum olfactorium (HOLMGREN, 1922). KAPPERS (1921) states, "In frühern Arbeiten habe ich sie Nucleus taeniae genannt" (p. 976). In Teleosts and Ganoids the nucleus is according to KAPPERS (1907) located ventro-laterally in the exverted parts of the telencephalon (tuberculum

taeniae). HOLMGREN (1922) points out that the nucleus in Selachians and Dipnoans is a derivative of the tuberculum olfactorium and according to the same author this also holds true for Ganoids and Teleosts.

As BERGQUIST states, the nucleus taeniae in the last mentioned animals is in contact with the nucleus ventralis thalami, and receives cells from pars frontalis thalami. In Selachians and Dipnoans there does not exist any such contact. The nucleus taeniae is exclusively a telencephalic structure, representated by the most caudal parts of the cortex of the tuberculum olfactorium. If a contact with thalamic centers ever existed in these groups, the development of the specific characteristics of the adult brains (prolongation of the telencephalon medium in Selachians, the great ventral growth of the hemispheres in Dipnoans) must have caused a separation, which, however, is not in any way documented by the ontogenetic development.

SEPTUM.

Adult conditions.

It has been stated that the peculiar shape of the tubercular parts is a very characteristic feature of the forebrain of Dipnoans, and the same holds true for the septal formation. The cellular arrangement in this structure, which constitutes practically the whole medial hemispheric wall, is somewhat different in various parts of the same.

In a section through the anterior part of the hemisphere (fig. 21 D), the medial hemispheric wall is characterized by having a thin ventricular layer of cells, containing small, darkly stained nuclei. Externally to this appears a layer of scattered cells which are greater in size and paler in colour. In the dorsal parts of this scattered layer there exists a cell-condensation having the form of a small cluster of cells (*p.c.n.o.a.*, fig. 21 D). Reading the sections in a rostral direction, this structure is situated ventro-medially to the olfactory bulb, and becomes connected to the ventro-medial parts of the granular layer of this structure (*p.c.n.o.a.*, fig. 21 A—D).

Ventrally to the above mentioned cell-cluster the layer of scattered cells becomes more pronounced and constitutes a cell-column which almost reaches the hemispheric surface (*n.l.s.*, fig. 21 D). On a transverse section about halfway between the anterior and posterior parts of the hemisphere, the medial wall is divided into a dorsal and a ventral part, the ventricular boundary between them being indicated by a sulcus septalis (*s. s.*, fig. 29 A). Pars dorsalis has the same cellular arrangement as all parts of the medial wall situated just caudal to the olfactory bulb. In the scattered layer the dorsal cell-cluster and broad column of cells are clearly distinguished (*p.c.n.o.a.*, *n.l.s.*, fig. 29 A).

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Pars ventralis is characterized by having a rather well developed ventricular layer with very few scattered cells outside it. Its ventral boundary with the ventro-medial parts of the tuberculum olfactorium is indistinct. It may be drawn immediately dorsal to the dorsal extension of the ventro-medial cells (*v.m.c.*, fig. 29 A) .

In the caudal half of the hemisphere, sulcus septalis is heavily ependymated (fig. 29 B), and has moved in a dorsal direction. The extension of pars dorsalis has diminished. The ventricular layer is more developed, and the dorsal cluster of cells has disappeared. Pars ventralis has increased, and now is distinguished by having a cortical cell-lamina outside the ventricular layer (*n.m.s.*, fig. 29 B).

Following the section in a caudal direction it is evident that pars dorsalis becomes more and more compressed between angulus dorsalis and sulcus septalis. Its caudal parts (*p.d.s.*, fig. 29 C) do not contain any scattered cells, and when the sulci septales of the two hemispheres break through the medial wall at the foramen of Monroi, the pars dorsalis is obliterated and is replaced by the epithelial lamina (septum ependymale), which constitutes the origin of the plexa of the lateral and third ventricle (*p.d.s., s.ep.*, fig. 9 D). No part of the nervous septal wall in the adult brain is thus situated dorsally to this foramen. Pars ventralis also diminishes, and just in front of the foramen Monroi is replaced by the nucleus of the anterior commissure (*n.c.a.*, figs 9 D, 29 D).

The cells of the septal formation are similar to those in the tuberculum olfactorium. The ventricular cells have brush-like dendritical branches, which, however, are somewhat coarser than in the corresponding structure in the tuberculum olfactorium. The scattered cells have very powerfully developed dendrites which extend over a considerable area. The most external of these cells remind one somewhat of the cortical cells in pallium. The neurites run into the fibre layer between the scattered cells in pars dorsalis and outside the ventricular layer in pars ventralis. In the ventral parts of the latter some of the neurites constitute a subependymal plexus which is connected with the same structure in the ventro-medial parts of the tuberculum olfactorium.

In Lepidosiren, Elliot Smith (1908) distinguishes a corpus paraterminale in the dorsal parts of the medial wall. This corresponds to pars dorsalis septi in Protopterus. The corpus paraterminale has the same cell-cluster in the dorsal parts of the scattered cell-layer which also contains a broad cell-column almost reaching the medial hemispheric surface. This is evident from Elliot Smith's figs 2 and 3. There exists a sulcus septalis distinguished by having its caudal parts powerfully ependymated. This sulcus separates the ventral part of the septal formation, corresponding to a pars ventralis septi of Protopterus, from the dorsal. Concerning these parts Elliot Smith states: "There can be no doubt that the dorsal segment of the body — from its structure and relations — is still paraterminal, but at a first glance, the identity of the

ventral segment is not so sure, chiefly for the reason that there is no clear line of demarcation between it and the corpus striatum (with the tuberculum). But when we reach figure 16 and find that it (the ventral segment) behaves in the same way as the paraterminal body is known to do in other vertebrates (i.e., fuses with its fellow to form the commissure-bed, which appears as a thickening of the lamina terminalis) its homology is established" (p. 533).

HOLMGREN (1922) points out that in Protopterus the medial wall is subdivided in a dorso-rostral and a ventro-caudal part. The former, "the fimbrial portion of the septum", is "filled up by more or less scattered cells derived probably from the ventricular wall of the fimbrial portion. These cells represent probably the nucleus lateralis septi. In the postero-ventral part of the septum the medial border of the tuberculum olfactorium is situated. This border is continued dorsally by a lamina of scattered cell-groups, representing probably a nucleus medialis septi" (p. 420).

GERLACH (1933) also subdivides the medial hemispheric wall in a dorsal and a ventral part ($B_4 + B_4'$). These, however, do not strictly correspond to my pars dorsalis and ventralis septi. GERLACH points out that his parts are separated from each other by a groove (fb_4), which, judging from his figures, is situated dorsally to sulcus septalis (fb_3 of Gerlach). The groove fb_4 is not a constant feature in the forebrain of Protopterus. In some specimens there is a broad but shallow depression in the ventricular wall of the pars dorsalis septi, opposite the column of scattered cells. It seems to me, however, that the sulcus septalis constitutes a more natural boundary, judging from the cellular arrangement on both sides of it. GERLACH points out that "Nuclei lateralis und medialis septi wurden nicht bemerkt. Möglicherweise entsprechen der Nucleus medialis septi" (of HOLMGREN) "Teile der Cortex olfactoria pars medialis".

In Epiceratodus HOLMGREN and VAN DER HORST distinguish a septum which like the conditions in Protopterus and Lepidosiren is subdivided by means of an oblique sulcus septalis into a pars dorso-rostralis and a pars ventro-caudalis septi.

Development.

The ontogenetic development of Protopterus has shown that pars dorsalis differentiates earlier than pars ventralis (p. 26). In Stage 5 the nervous parts of the medial wall just in front of the septum ependymale is built up by pars dorsalis, which has a broad connection with the granular cells of the tuberculum olfactorium. In this stage the ventricular cells reach the medial hemispheric surface. During the development, the dorsal cell-cluster develops out of the medial parts of the granular layer in the bulb (*p.c.n.o.a.*, fig. 34 B), and fibres begin to appear outside to and among the outer layers of the ventricular cells of pars dorsalis. These outer layers, because of the fibres penetrating

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them, become split up and thus the scattered cells of pars dorsalis septi make their appearance (*p.d.s.*, fig. 34 B). The ependymated parts of the sulcus septalis almost reach the medial hemispheric surface and separate the pars dorsalis from more ventrally situated cell-layers (fig. 34 B). When foramen Monroi breaks through in this stage (30 mm), pars dorsalis continues dorsally and caudally to this foramen, contrary to the conditions in the adult brain. Following the sections in a caudal direction (figs 31 C, 34 A, which represent a somewhat younger stage, but the conditions are the same as in the 30 mm stage shown in fig. 34 B) it is evident that pars dorsalis is replaced by the septum ependymale (*s.ep.*, fig. 34 A), except for its most dorsal part which persists in the form of a dorsal caudal continuation of the pars dorsalis septi. In fig. 34 A it is situated ventrally to the most caudal parts of the bulbar primordium (*p.f.s.*), and behind this structure it is possible to trace the pars dorsalis a short distance ventrally to the medial pallial parts. This caudal extension of pars dorsalis septi, situated dorsally and caudally to the foramen Monroi and the septum ependymale represents an embryonic pars fimbrialis septi. In the adult brain this structure becomes obliterated as a result of the powerful rostral prolongation of the dorsal parts of the hemisphere, which causes all parts behind and dorsal to the foramen Monroi to be drawn in front of it.

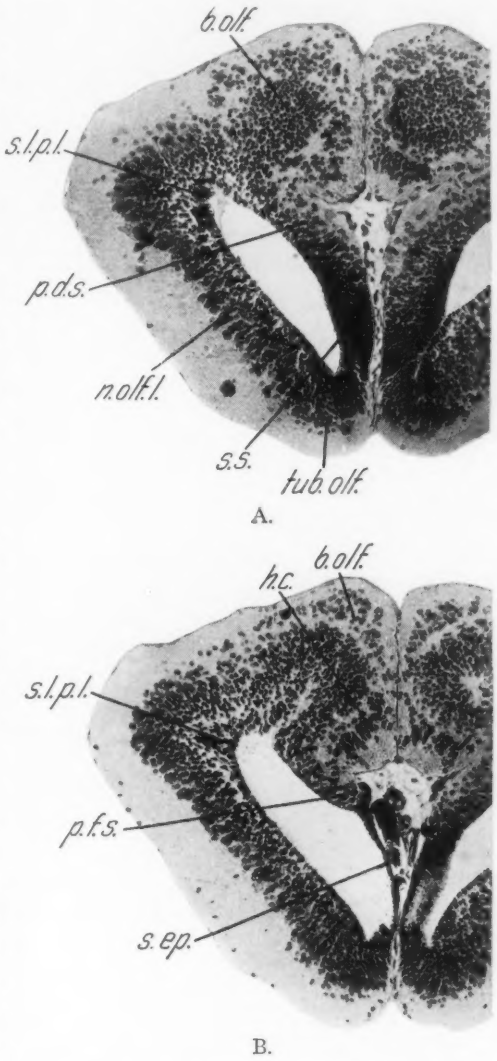

Fig. 41 A—B. *Epiceratodus Forsteri*. 28.5 mm; transv. sect. just in front of the septum ependymale. B transv. sect. at the level of the same structure; 60x. AZAN-MALLORY.

Similar conditions exist in Epiceratodus (cf. fig. 41 A—B), in which we find the caudal parts of the pars dorsalis ventrally to the primordium hippocampi and dorsally to the septum ependymale (*p.f.s.*, fig. 41 B). This embryonic pars fimbrialis septi corresponds exactly to the same structure in adult Amphibians, where it is situated between the ventral parts of primordium hippocampi and the septum ependymale (cf. the figs 10—11 of HERRICK, 1927).

Pars ventralis develops between Stages 5 and 6 out of the cellular parts ventro-medially to the angulus ventralis. It is separated distinctly from pars dorsalis by the ependymal portion of the septal sulcus (fig. 34 B), but it is not possible to distinguish any clear boundary with the primordium of the tuberculum olfactorium. In Stage 6 cells have migrated out of the ventricular layer of pars ventralis, and in a 35 mm larva these cells are arranged in a dorso-ventrally extended cell-lamina, situated immediately inside the medial hemispheric surface (*n.m.s.*, fig. 42). Ventro-laterally to this lamina there also appear groups of migrated cells (*v.m.c.*, fig. 42), which begin still more caudally to arrange themselves into the ventro-medial parts of the tubercular cortex.

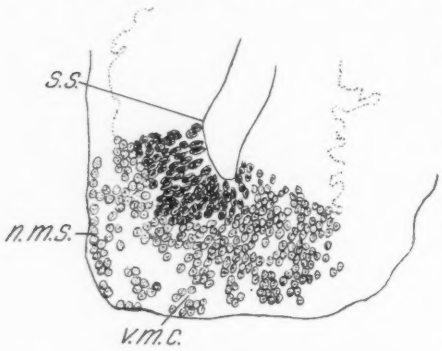

Fig. 42. *Protopterus annectens.* 35 mm; transv. sect. through the ventro-medial part of the hemisphere at the level of the nucleus medialis septi; 100x. AZAN-MALLORY.

The septal nuclei.

According to HOLMGREN (1922) there exists in Polypterus a "great bulbar ventricle opening into the medial forebrain with a foramen monroi-like opening". This ventricle is limited ventrally by a subpallial part which "forms a small subpallial septum (fig. 36, sp). In this septum enters a process of the nucleus olfactorius anterior .... The cells in this process stain somewhat darker than those of the anterior olfactory nucleus. The process comes from the ventro-medial part of the granule-cell layer...." (p. 424). HOLMGREN has also observed this pars precommissuralis in Teleosts. "A nucleus olfactorius anterior pars precommissuralis I have found in Osmerus in the same position as in Polypterus, but extending further backwards. In ganoids I have found no such nucleus" (HOLMGREN 1922, p. 429).

In Protopterus there exists a structure which reminds one very much of this pars precommissuralis, i.e., the cell-cluster in the dorsal parts of pars dorsalis (*p.c.n.o.a.*, fig. 21; 29). It constitutes a string of cells which is in contact rostrally with the ventro-medial parts of the granular cell-layer of the bulbus olfactorius, and also is characterized by having more darkly stained

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cell-nuclei. This pars precommissuralis of nucleus olfactorius anterior[1] also corresponds to a similar structure in Epiceratodus, indicated by HOLMGREN and VAN DER HORST as a nucleus lateralis septi. In this species it "begins in the most caudal part of the olfactory crus, ventral to the ventricle. As the ventricle of the crus opens in the lateral ventricle the nucleus is found more medially and caudally in septum at the dorsal border of this brainpart. This position it holds nearly to the foramen Monroi..... The nucleus lateralis septi is in its whole extent free from the ventricular cell-layer" (p. 74). This description of the lateral septal nucleus in Epiceratodus could also be valid of the pars precommissuralis of the granular cell-layer in Protopterus, except for the fact that, nucleus lateralis septi in Epiceratodus does not have any direct contact with the cell-layer in the olfactory bulb. The ontogenetic development of this species, however, clearly shows the existence of a contact (fig. 13 C; 14 C) between pars dorsalis septi and the bulbar formation. The lateral septal nucleus in Epiceratodus differentiates very late in the ontogenetic development, and because of the absence of later developmental stages in my material I have not been able to verify whether this nucleus differentiates out of the contact between the pars dorsalis and the granular layer of the olfactory bulb, as is the case in Protopterus. It seems to me however that the position and structure of pars precommissuralis in Protopterus and nucleus lateralis septi in Epiceratodus speaks in favour of these structures being homologous.

In Epiceratodus there exists a nucleus intermedius septi which "begins in the frontal fourth of the septum a little below the nucleus lateralis septi" (HOLMGREN and VAN DER HORST, 1925; p. 75). The authors state that in Epiceratodus this nucleus lies on each side of a shallow sulcus which caudally "becomes more flattened out and disappears". Nucleus intermedius corresponds in position and extension to the column of scattered cells in pars dorsalis of Protopterus. As has already been stated above there exists in some specimens a shallow sulcus which is situated in the medial ventricular wall opposite to this structure. It is only distinct rostrally. An investigation of the forebrain of adult Epiceratodus shows that nucleus intermedius septi does not constitute a distinct nucleus, clearly separated from the ventricular layer. It appears as a column of scattered cells connected medially with the ventricular layer, analogous to the conditions in Protopterus. In Selachians and Amphibians the nucleus lateralis septi is in immediate contact with the ventricular layer. In forms with a distinct sulcus septalis it lies along its whole extension dorsally

[1] HOLMGREN (1920, 1922) identifies the granular layer of the olfactory bulb as a nucleus olfactorius anterior. HERRICK in his works on Amphibians (i.a., 1933 a) identifies this nucleus as a "zone of relatively undifferentiated tissue which encircles the olfactory bulb" (p. 133). Thus this anterior olfactory nucleus does not corresponds strictly to the same nucleus in HOLMGREN, and because of this I prefer to indicate the ventricular layer of the bulb as the granular layer. I retain, however, HOLMGREN's name for the caudal extension of the ventro-medial parts of this layer, i.e., pars precommissuralis of nucleus olfactorius anterior.

to this sulcus. Of the two septal nuclei in pars dorsalis septi in Dipnoans the nucleus intermedius septi in Epiceratodus and the column of scattered cells in Protopterus are more related to the ventricular layer in as much as they are not clearly separated from the same. They are also situated along their whole extension dorsally to the sulcus septalis. These conditions seem to me to indicate that the structures in question are homologous to the nucleus lateralis septi in Selachians and Amphibians.

Outside the ventricular layer of the pars ventralis septi exists in Epiceratodus a nucleus medialis septi which caudally almost reaches the level of the foramen Monroi. Rostrally it begins at about the caudal third of the septum. In Protopterus, pars ventralis septi contains a distinct nucleus externally to and well separated from the ventricular layer. This according to HOLMGREN (1922) corresponds to a nucleus medialis septi. GERLACH (1933) is of the opinion that this structure probably constitutes the medial parts of the cortex of the tuberculum olfactorium.

A cursory investigation certainly speaks in favour of it being a dorso-medial continuation of this cortex. Against such a conception, however, speak the following facts:

1. no direct contact exists between the nucleus medialis septi and the ventro-medial parts of the tubercular cortex, the ventral parts of the former being situated distinctly medial to the cortex. As indicated by fig. 9 D this latter structure is horizontal while the medial septal nucleus extends dorso-ventrally;

2. it may constitute a remnant of a former tubercular cortex being a medial parallel to the isolated cell-clusters in the lateral hemispheric wall. Ontogenetic conditions, however, argue against this as the nucleus in question develops out of pars ventralis septi in form of scattered cells which migrate towards the medial hemispheric surface and there arrange themselves into a cortical lamina, but they do not develop out of a well defined cell-condensation in the outer layer of the ventricular cells as is the case with the cell-clusters in the lateral wall (see p. 111).

3. the fibre connections argue against GERLACH's conception because tractus septo-habenularis (see p. 127) receives fibres from pars dorsalis, pars ventralis, and nucleus medialis septi. This tract is well separated from the habenular connections of the tuberculum olfactorium (tractus olfacto-habenularis ventralis);

4. in Epiceratodus the nucleus medialis septi clearly corresponds to the same structure in Protopterus in as much as it has exactly the same position, and as there does not exist any tubercular cortex in the adult forebrain of Epiceratodus it cannot constitute a dorso-medial continuation of such a structure. If it should be a remnant of an older cortical structure belonging to the tuberculum olfactorium it is very curious that all parts of the tubercular cortex except its dorso-medial component have been reduced in this species.

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Because of the facts mentioned above I do not consider the nucleus medialis septi in Protopterus to be a more or less isolated dorso-medial component of the cortex of the tuberculum olfactorium.

In Selachians, nucleus medialis septi, according to HOLMGREN (1922), constitutes a cell-lamina in the medial hemispheric wall dorsally to the medial part of the tubercular cortex in these forms. In the caudal parts the nucleus consists of a dorsal and a ventral part. The former "forms an unpaired cellmass around the base of the recessus neuroporicus". The ventral part "diverges from the dorsal, and at the level of the front part of the foramen Monroi it is found in the middle of the basal septum, where it is seen in cross-sections as a rather well-delimited nucleus ....." (p. 411).

Compared with the conditions in Dipnoans, the septal formation in Amphibians is very compressed, and a sulcus septalis is often lacking. In Amblystoma the telencephalic centers seem to be fairly well developed, and HERRICK (1927) states that in the medial ventricular hemispheric wall of this form there exists a sulcus limitans septi. The position of this sulcus corresponds to the sulcus septalis in Dipnoans. The parts situated ventrally to this sulcus he indicates as a nucleus accumbens which HERRICK includes in the septal formation. Dorsally to the sulcus the medial wall contains a ventricular nucleus lateralis septi and externally to this a nucleus medialis septi (figs 5—9, HERRICK 1927). In the rostral part of the hemisphere there exists a nucleus olfactorius anterior, and in the medial wall this nucleus is continued caudally by nucleus medialis septi. In the caudal half of the medial wall the medial septal nucleus is quite free from the ventricular cell-layers, and just in front of septum ependymale it is divided into a dorsal pars fimbrialis septi and a ventral part, which, beneath the foramen Monroi, "has merged with the bed nucleus of the decussation of the medial forebrain bundle except for a narrow band of small cells next to the medial fissure, which retains its individuality" (p. 263). Nucleus medialis septi in Amblystoma reminds one, therefore, of the same nucleus in Selachians, which in its caudal parts is divided into a dorsal and a ventral part, the latter being situated ventrally to the foramen Monroi.

HOLMGREN (1922) points out that the position of the pars precommissuralis of nucleus olfactorius anterior in Polypterus argues in favour of this nucleus representing a nucleus medialis septi, "this nucleus being many times a backward continuation of the nucleus olfactorius anterior or lobus olfactorius". According to SÖDERBERG similar conditions exist in Amphibians, in which group the medial septal nucleus "originates from the granular cell-layer of bulbus olfactorius ... This septal nucleus appears to be homologous with the nucleus which in teleosts is termed nucleus olfactorius anterior pars precommissuralis, which is also derived from the bulbar part of the brain, a fact pointed out by HOLMGREN (1920)" (p. 107).

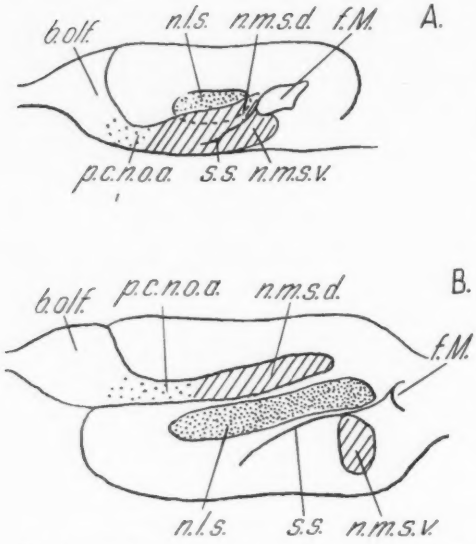

Fig. 43. Schematic drawing of the septal nuclei in an Urodele (A) and in Protopterus (B). The hemispheres are seen from the medial side.

In Dipnoans, nucleus medialis septi is well differentiated, but, compared with the extension of the septal formation, only contains a relatively small area. It is wholly confined to the pars ventralis ventrally to the sulcus septalis, and thus corresponds to the ventral caudal parts of nucleus medialis septi in Selachians and Amblystoma. It does not, however, extend caudal to the foramen Monroi as in these forms. Unlike the conditions in the Amphibians, there does not exist any contact between nucleus medialis septi and the bulbar formation. This difference may be due to the powerful rostral and ventral extension of the hemispheres, which could have caused a separation of the dorsal and the ventral parts of the nucleus medialis septi (fig. 43). The pars precommissuralis of the anterior olfactory nucleus of Dipnoans should thus contain in its caudal parts the equivalent of the dorsal caudal parts of the medial septal nucleus in Selachians and Amphibians. A suggestion that this is the case may be found in Epiceratodus, as HOLMGREN and VAN DER HORST have observed that the cells of pars precommissuralis (nucleus lateralis septi of the authors) are somewhat different in appearance rostrally and caudally. "Frontally it is composed by relatively great cells, towards the foramen Monroi the cells become smaller and more densely arranged". In Protopterus also the foremost parts situated immediately adjacent to the caudal bulb have greater cells with more palely stained nuclei. In the caudal parts of the pars precommissuralis the cells are smaller, more darkly stained and lie closely together. In nucleus medialis septi of Protopterus the cellular conditions correspond to those found in the posterior parts of pars precommissuralis.

Fibre anatomy.

The most conspicous fibre mass in the medial hemispheric wall is the medial forebrain bundle, outside pars ventralis septi. It contains fibres from all parts of septum which are arranged in a row of bundles one over the other (fig. 29 A). At the level of the nucleus medialis septi these bundles are situated

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between the nucleus and the ventricular layer of pars ventralis (fig. 29 B). In a caudal direction these bundles merge and immediately rostral to the level of the anterior commissure they have fused into a solid mass of fibres which enters the dorsal parts of this commissure. It is possible to distinguish a dorsal and a ventral part of this fibre mass. The former contains crossing fibres between the septal formations of the two hemispheres, and constitutes a commissura septi (*c.s.*, fig. 29 G). This commissure also contains the fibres of the commissura interbulbaris (see p. 82).

The ventral component contains decussating fibres, which, after leaving the commissure, assemble medially to the caudal parts of the tubercular cortex (*Tr.olf.hyp.m.*, fig. 29 D). These fibres together with uncrossed fibres from the medial forebrain bundle constitute a tractus olfacto-hypothalamicus medialis. It very soon merges with the ventral and lateral olfacto-hypothalamic tracts and, somewhat caudally to the level of the anterior commissure, these three tracts together constitute a dense fibre mass outside the ventricular layer of the pars inferior of the preoptic nucleus (*Tr.olf.hyp.l.+m.+v.*, fig. 29 F). Tractus olfacto-hypothalamicus medialis corresponds to a similar tract in Epiceratodus (Holmgren and van der Horst, 1925).

As was stated above, the medial forebrain bundle passes between the ventricular layer of pars ventralis septi and nucleus medialis septi. Between this nucleus and the medial hemispheric surface there exists another very well defined tract, also containing fibres from all parts of septum, including the medial septal nucleus (*Tr.s.h.*, fig. 29 B). This tract runs down ventrally and, at the level of the anterior commissure, is situated medially to the tractus olfacto-hypothalamicus medialis (*Tr.s.h.*, fig. 29 D). Reading the sections in a caudal direction we find the tractus somewhat more laterally, and at the level of the entrance of the posterior ramus of the terminal nerve it is situated laterally to the same (*N.t.p.*, *Tr.s.h.*, fig. 29 E). Caudally to the anterior commissure the tract lies outside the combined olfacto-hypothalamic tracts (fig. 29 F), and the fibres begin to run upwards in a dorsal direction to join the stria medullaris complex. The tract connects the septal formation with the habenula and constitutes a tractus septo-habenularis. In the hemispheric parts this tract also contains fibres belonging to the "diagonal band of Broca" already described (p. 98).

Ventrally to the foramen Monroi the pars ventralis septi meets the corresponding structure in the opposite hemisphere, and this union constitutes a bed nucleus of the anterior commissure. It consists of a lamina of cells dorsally to the commissural fibres (*n.c.a.*, fig. 29 D, G). These cells have long slender dendrites arborizing in a well defined neuropilar mass ventrally to the commissure. This neuropil contains collaterales from the ventral and medial forebrain bundles.

NUCLEUS PREOPTICUS.

Adult conditions.

The hemispheric centres in the forebrain are separated from the diencephalon by an unevaginated part, the telencephalon medium. In Selachians and especially in Holocephalians this brainpart is powerfully elongated. In Dipnoans it is rather short and resembles more closely amphibian conditions. The telencephalon medium in Protopterus is built up by the nucleus preopticus, which, as a result of the cellular arrangement can be divided in two parts, pars superior and pars inferior.

Pars superior constitutes the dorsal parts of the telencephalon medium, and is characterized by having a ventricular layer split up into dorso-ventrally extended cell-laminas parallel to each other (*n.pr.p.s.*, fig. 29 E—F). Rostrally the cell-layer is more compact, and passes over without any distinct boundary into the caudal parts of the nucleus olfactorius lateralis.

Pars inferior is situated on each side of the sulcus preopticus and extends between the chiasma and the anterior commissure. The ventricular layer differs from the same structure in pars superior in having densly packed cells (*n.pr.p.i.*, fig. 29 F). Rostrally the nucleus has a cellular process situated beneath the caudal parts of the anterior commissure (*n.pr.p.i.*, fig. 29 E, G).

HOLMGREN and VAN DER HORST have shown the existence of a pars inferior and a pars superior of the preoptic nucleus in Epiceratodus. The authors state that in Protopterus there exists an ependymated boundary groove between the two parts of the preoptic nucleus. I have not been able to find any such groove in my specimens. Sometimes, however, the rostral parts of the lightly ependymated sulcus preopticus are located rather high up in the ventricular wall, and as a result of this the dorsal and rostral parts of the sulcus may hold positions approximately on the border between pars inferior and superior. Usually, however, the sulcus is located along its whole extension in the ventricular wall of pars inferior.

GERLACH (1933) is of the opinion that the division of the preoptic nucleus does not constitute a correct interpretation of the conditions in the dipnoan group. "Das Gebiet welches bei Holmgren und van der Horst mit 'Nucleus praeopticus pars dorsalis' bezeichnet ist, gehört nach der Ansicht des Verfassers zum Teil zum ventralen Thalamus und stellt eine Eminentia thalami dar, zum anderen Teil zur Massa cellularis reuniens des Übergangsgebietes; wenigstens ist dies bei Protopterus der Fall" (p. 382). According to GERLACH the ventral part of the preoptic nucleus belongs to diencephalon, and he, therefore, indicates pars inferior, as the anterior part of a "Regio hypothalamicus". Concerning the di-telencephalic border GERLACH states further: "Um seine

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Grenze gegen das Diencephalon zu bestimmen, begrentzt man durch das Velum transversum und eine ungefähr durch die Mitte der Commissura anterior senkrecht zur Hirnachse gezogene Gerade eine Fläche, welche die Grenzfläche der beiden Vorderhirnderivate darstellt" (p. 316).

RÖTHIG (1923) has a somewhat similar conception. In describing the diencephalon of Amphibians, he presents the different points of view set forth by the authors concerning the di-telencephalic border, and he remarks that "Unter all diesen Umständen kann für die Frage der Grenzführung zwischen beiden eine Furche erhöhte Bedeutung gewinnen, die vom Rec. praeopt. in der Richtung zum Velum trans. zieht, der Sulcus intraencephalicus anterior von v. Kupffer....." (p. 621). RÖTHIG is of the opinion that this groove constitutes a di-telencephalic boundary groove, and thus there exists "einer Grenzführing vom Velum trans. zur Vorderwand des Rec. praeopt....".

KUHLENBECK (1924) states that "Nur der Abschnitt der Lamina terminalis, welcher die commissura anterior enthält und der Anteil dorsal der Kommissure sind zum Telencephalon zu rechnen und nehmen bei manchen Vertebraten an das Bildung einen unpaaren Endventrikels teil....." Kuhlenbeck bases his view on HOCHSTETTER's investigation of the ontogenetic development of the human brain (1919). The telencephalic primordium is separated from diencephalon by means of an outer "sulcus hemisphäricus", which corresponds to a ventricular ridge "den man Torus hemisphäricus bezeichen könnte. Ventral- und oralwärts läuft letzerer flach gegen die Kommissurenplatte aus, dorsalwärts setzt er sich in einer Falte fort, welche den Velum transversum der niederen Vertebraten entspricht" (KUHLENBECK, 1924).

The ontogenetic development of Dipnoans and Amphibians has shown that there exists a ventricular ridge in the anterior parts of the primitive forebrain, which constitutes a boundary between di- and telencephalic primordia. This ridge extends between velum transversum and the chiasmatic ridge, not the ridge of the anterior commissure, which according to HOCHSTETTER is the case in human embryos. The ontogenetic development shows further that the preoptic nucleus develops a r o u n d the ventral parts of the intraencephalic sulcus, between commissura anterior and the chiasma, and i n f r o n t o f the di-telencephalic ridge. RÖTHIG's conception that the sulcus intraencephalicus anterior is a di-telencephalic boundary groove, only holds true for its dorsal part, which in later stages by fusing with the sulcus diencephalicus ventralis, constitutes the dorsal boundary of the preoptic nucleus. In the adult brain the di-telencephalic boundary in Dipnoans is thus defined by velum transversum, the anterior parts of the ventral diencephalic sulcus and the optic chiasma.

The groove which GERLACH indicates in his fig. 14 as a sulcus diencephalicus ventralis (*s.d.v.*) is in reality a caudal continuation of the angulus ventralis of the lateral ventricle (see p. 57). The ventral diencephalic sulcus is situated

high up in the ventricular wall at the level of the plexus of the third ventricle in GERLACH's fig 14. Because of this GERLACH has cut off the pars superior of nucleus preopticus from the telencephalon, and has not been able to get his results to correspond to those of HOLMGREN and VAN DER HORST on Epiceratodus.

Pars superior and the corresponding structure in other lower vertebrates.

As stated by HOLMGREN and VAN DER HORST, pars inferior must be considered as the "nucleus preopticus proper",[1] but what then is pars superior? It certainly constitutes a transitory area between the hemispheric parts of the forebrain and the diencephalon. According to JOHNSTON (1911 a) the greatest part of telencephalon medium in Selachians contains a "primordium pallii somatici". Dorsally this structure reaches the taenia fornices. Rostrally it joins the nucleus olfactorius lateralis and area superficialis basalis (tuberculum olfactorium). Ventrally it is bordered by the precommissural body (septum) and nucleus preopticus. This latter nucleus "consists of central gray lining the recessus preopticus between the optic chiasma and the anterior commissure", that is, it has the same extension as pars inferior of the preoptic nucleus in Dipnoans. "Primordium pallii somatici" or "area somatica" corresponds in its position to the pars superior of the preoptic nucleus in the same group. JOHNSTON points out that "the justification for calling this a somatic area lies in the entrance of ascending tracts from the visual and general sensory centres in diencephalon". From another investigation by the same author (1911 b), it also is evident that in Ganoids and Teleosts the area somatica is placed dorsally to the preoptic nucleus and constitutes a transitory area between forebrain and diencephalon. HOLMGREN (1920) confirms JOHNSTON's conception that area somatica in Teleosts is homologous to the corresponding structure in Selachians.

As in fishes with evaginated hemispheres, the ventral parts of the telencephalon medium in Amphibians consists of a nucleus preopticus, extending between the commissura anterior and the chiasma. Dorsally to this nucleus there exists an area inserted between the hemispheric centres and the diencephalon. The structure in question has been thoroughly investigated by HERRICK (1921 b, 1927, 1933 a) and this "strio-amygdaloid complex" constitutes a primordium of corpus striatum and nucleus amygdala, and corresponds in position to the area somatica of fishes.

Ontogenetically the pars superior of nucleus preopticus develops out of the caudal telencephalic proliferation zone on the border between the pallial area and the primordium of nucleus preopticus (pars inferior). In later stages,

[1] This opinion is supported by JENER (1930).

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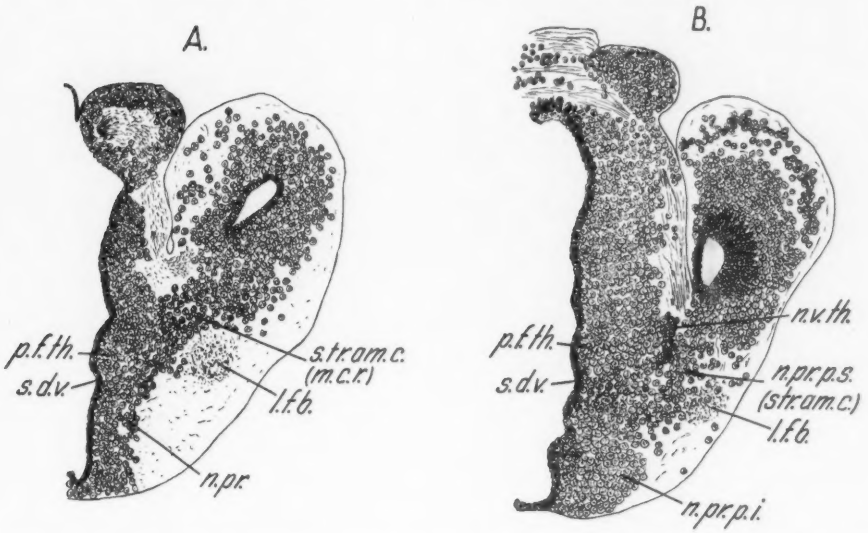

Fig. 44. Transv. sect. through the caudal parts of telencephalon and neighbouring parts of diencephalon in Triturus (24 mm; A) and Protopterus (18 mm; B); 70x. AZAN-MALLORY.

when the hemispheres have a well developed caudal lobe behind the foramen Monroi (pars postforaminalis), pars superior constitute an area inserted between the ventral parts of the pallium and the pars inferior. As is evident from fig. 44, pars superior of the dipnoan forebrain corresponds to a cellular area in an urodele larva of the same stage of development, an area which connects the pallial parts with nucleus preopticus and the neighbouring parts of the ventral thalamus. This is the "massa cellularis reuniens" of RÖTHIG (1923), indicated by HERRICK in Amblystoma (1927) and Necturus (1933 a) as a nucleus amygdala.

In the adult forebrain of Protopterus the caudal parts of the nucleus olfactorius lateralis passes over without any distinct boundary into the pars superior. As has already been mentioned (p. 108), there probably exists a primordium of a corpus striatum in this caudal part of the lateral olfactory nucleus, and this primordium together with the pars superior of the preoptic nucleus in Protopterus corresponds in position and development to the "strio-amygdaloid complex" of Urodeles.

In a number of works (1921 b, 1927, 1933 a) HERRICK has put forth his results concerning the fibre-anatomical structure of the strio-amygdaloid complex. The conditions in Amblystoma (1927) are quoted below (p. 302):

> "1) an olfactory component, perhaps directly from the olfactory tract by way of a ventrolateral olfactory tract as in the frog, and certainly indirectly from the dorso-lateral olfactory nucleus;

2) a septal connection by way of the diagonal band of Broca, though these fibres make their chief connection with the dorso-lateral olfactory nucleus;

3) a commissural connection;

4) short correlation fibres connecting with all neighbouring parts;

5) a strong tractus amygdalo-habenularis;

6) ascending sensory radiations of somatic type from the pars dorsalis thalami by the tractus thalamo-frontalis;

7) hypothalamic connections by the olfactory projection system."

In Protopterus, pars superior seems to be a caudal continuation of the powerfully developed correlation center represented by the caudal parts of the nucleus olfactorius lateralis (primordium of corpus striatum). Between the very pronounced network of dendritical arborizations outside the ventricular layer of pars superior, there run longitudinal fibres belonging to the system of the lateral forebrain bundle. As has already been stated (p. 104) some of these fibres are arranged in distinct bundles but most of them constitute a dense fibre mass filling up the stratum album outside the superior nucleus. As a result of the occurence of endbranches and collaterales from this fibre mass there has developed a dense neuropil corresponding to a similar structure in urodeles (amygdaloid neuropil; HERRICK, 1927, 1933 a).

An investigation of the fibre connections of pars superior compared, with HERRICK's results from Amblystoma has given the following results:

1) A direct connection with the olfactory bulb by means of the tractus olfacto-ventrolateralis (is possible to distinguish in Weigert-preparations). As a result of the absence of distinct bundles, I have not been able to follow any fibres from the primordium pyriforme (the dorso-lateral olfactory nucleus of HERRICK) to the pars superior, but as they run down into the fibre mass of the lateral forebrain bundle and follow this in a caudal direction, it is very probable that there exists in Protopterus the same indirect olfactory connection as in urodeles;

2) I have not been able to identify any direct septal connection. Pars superior, however, is not separated distinctly from the striatal primordium, and it is possible that some of the septal fibres to the caudal parts of the latter area do in reality reach the pars superior;

3) from pars superior fibres run down into the anterior commissure;

4) fibre connections between pars superior and nucleus olfactorius lateralis, between the former and pars inferior, and fibres to the neighbouring parts of the thalamus;

5) from all parts of pars superior fibres extend upwards in a dorsal direction following the stria medullaris complex to the habenula;

6) The dorsal parts of pars superior receives neurites from cells in the neighbouring thalamic parts (these fibres, however, come from the pars frontalis thalami, HERRICK's pars ventralis thalami);

7) fibres run down into hypothalamus and are located together with ascending fibres from the same brainpart (olfactory projection tract).

The ontogenetic development, the position in the adult brain, and to a certain extent the fibre-anatomical conditions in Protopterus argue in favour of the pars superior of the preoptic nucleus, together with the caudal parts of the nucleus olfactorius lateralis, being homologous to the strio-amygdaloid complex of the Urodeles. In the latter group, however, the different nuclei in this complex are often rather well differentiated, unlike the conditions in Protopterus. In Amblystoma, HERRICK distinguishes primordia of a nucleus caudatus, a dorsal and a ventral striatal nucleus, and two amygdaloid nuclei. Necturus, however, is very little differentiated in these parts. "Here there is no differentiation comparable with the head of the caudate nucleus .... there is no obvious difference in the structure of the dorsal and ventral striatal gray, nor is the neuropil associated with the two parts so clearly separated or so highly organized as in Amblystoma" (HERRICK, 1933 a). Concerning the two amygdaloid nuclei of Amblystoma, they are represented in Necturus by an "undifferentiated amygdaloid primordium". In these conditions Necturus therefore corresponds more closely to Dipnoans.

The primordium of the strio-amygdaloid complex of Protopterus corresponds also to the area somatica in other groups of fishes. As in those it constitutes the dorsal parts of the telencephalon bordering the diencephalon, and receives ascending thalamic fibres.

Nucleus magnocellularis.

In the caudal parts of pars inferior of the preoptic nucleus there exists an area, bounded frontally by the sulcus preopticus, and containing cells characterized by their greater size and having paler nuclei. In preparations stained with cresyl-violet they are very easily distinguishable and appear as single cells or small clusters of cells scattered between the small, darkly stained cells of the ventricular layer of nucleus preopticus. This structure constitutes a nucleus magnocellularis (*n.m.c.*, fig. 45 A).

According to HOLMGREN and VAN DER HORST there exists caudally in pars inferior of Epiceratodus two great cells, which are situated directly above the optic ridge. These cells "represent perhaps a magnocellular part of the nucleus". CHARLTON (1932) in a specimen of Epiceratodus has observed a nucleus magnocellularis. "This has much the same position as found in the preteleosts having almost the same midpoint". According to CHARLTON nucleus

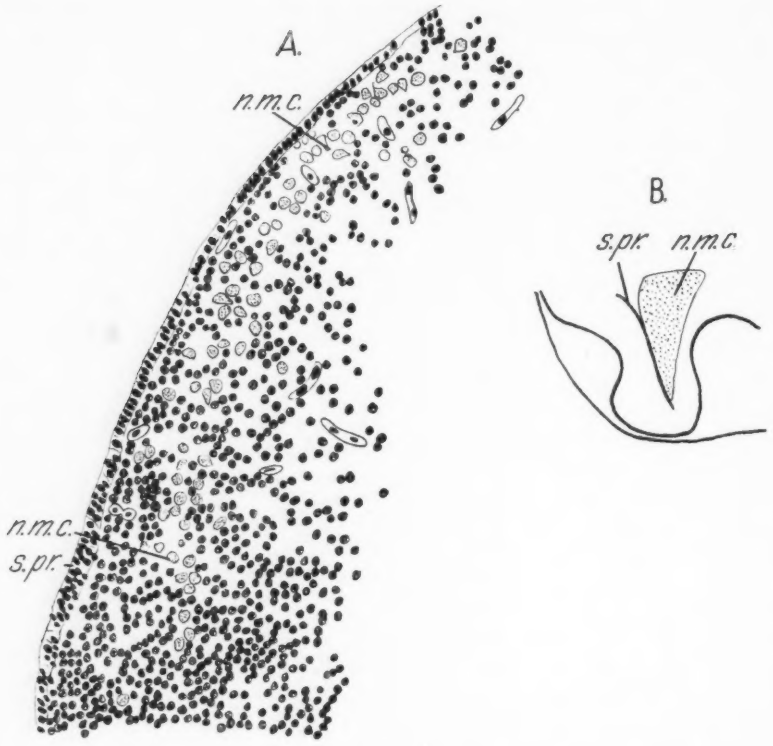

Fig. 45. *Protopterus annectens.* Adult; A transv. sect. through nucleus magnocellularis; 80x. CRESYL-VIOLET. B schematic drawing showing the position of the nucleus.

magnocellularis in fishes is situated "just lateral to the floor of the recess or in some cases beginning higher up along the sides of the recess and then dropping to the floor level, where it remains for a time. It begins in front of, and is located for the most part dorsal to the optic chiasma. Later it leaves the floor appearing more dorsal at each caudal section, to terminate as a narrow strand of perhaps a single cell in cross-section". The great cells in the caudal parts of the preoptic nucleus, "straight over the optic ridge" in Epiceratodus, seem to correspond to the most caudal parts of CHARLTON's magnocellular nucleus. I have investigated an adult specimen of Epiceratodus (HOLMGREN and VAN DER HORST's Stockholm specimen) but have not been able identify any part of the nucleus in front of HOLMGREN and VAN DER HORST's magnocellular structure. It may be due to the staining (Bielschowsky), as in Protopterus the magnocellular nucleus is very difficult to localize in brains stained by Bielschowsky's method.

Protopterus differs from other fishes in not having the broadest part of the nucleus along the floor of the preoptic recess but appearing instead as

a triangle with its apex turned ventralward (fig. 46 B). It reminds one of the nucleus magnocellularis in certain Urodeles (Amphiuma means), a fact which is evident from CHARLTON's investigation (1929, fig. 7). CHARLTON points out, however, that in Urodeles some species have a nucleus with an extension similar to that in Teleosts, that is, the broadest part of the nucleus is situated in the ventral parts of the preoptic recess almost at floor level, not the reverse as in Protopterus and Amphiuma.

Fibre Anatomy.

The fibre connections of the preoptic nucleus have already been described (p. 132), and I have only to mention the existence of fibres from the nucleus magnocellularis, which run ventro-caudally together with the hypothalamic connections of the nucleus preopticus, tractus preoptico-hypothalamicus. I have observed the magnocellular fibres in Bodian-preparations, but have only been able to follow them for a short distance. They probably correspond to the tractus preoptico-tuberis in Teleosts (SHELDON, 1912; HOLMGREN, 1920).

V. NERVUS TERMINALIS.

In the basal parts of the telencephalon medium, at the level of the foremost parts of pars inferior of the preoptic nucleus, the nervus terminalis, nerve of PINKUS (PINKUS, 1894, 1895, 1905), enters the brain (*N.t.p.*, fig. 29 E). This nerve, however, does not contain all fibres belonging to the terminal nerve complex. It only constitutes its posterior branch. HOLMGREN and VAN DER HORST have shown that in Epiceratodus the nervus terminalis has two components, an external terminalis posterior homologous to the nerve of PINKUS, and an internal terminalis anterior which "enters the olfactory tract on the medio-ventral side, just at the caudal end of the bulbar formation" (p. 84). This anterior root, which consists of several bundles, has a ganglion situated in the caudal parts of the olfactory crus. The authors point out that there probably exists an anterior root in Protopterus and Lepidosiren.

In Protopterus, this structure undoubtedly exists, and consists of a slender fibre bundle, situated among the medial bundles of the olfactory nerve which it follows caudally. It enters the brain immediately caudal to the olfactory bulb (*N.t.a.*, fig. 46). At this point there exists a small external aggregation of cells (*g.N.t.a.*, fig. 46), which in some specimens are rather scattered, in others more densely arranged. Caudally to this ganglion the anterior root appears at first as a collected bundle, which, however, very soon splits up in several very slender bundles which spread in the fibre layers of the medial hemi-

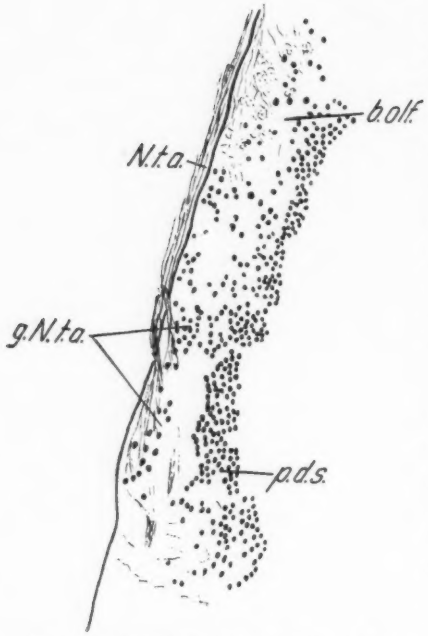

Fig. 46. *Protopterus annectens.* Adult; hor. sect. through the medial hemispheric wall at the boundary between the olfactory bulb and the septum; 60x. BODIAN.

spheric wall. In preparations stained by BODIAN's and BIELSCHOWSKY's methods, I have been able to follow these bundles in a caudal direction. Before reaching the level of the anterior commissure, the bundles break up into single fibres, and in no case I have found any fibre or fibre unit entering this commissure. This anterior root in Protopterus corresponds to the same structure in Epiceratodus.

Compared to the conditions in Epiceratodus the posterior root has a somewhat different appearance as it does not split up into bundles but constitutes a slender nerve, which is situated ventrally and entirely outside the hemispheres. Rostrally it follows the frontal wall of the endocranial cavity in a dorsal direction, and passes through this wall ventrally to the olfactory nerve. In front of this passage the posterior root has a ganglion. Rostrally to this it follows closely the olfactory bundles in a rostral direction. Unlike the conditions in Epiceratodus, the anterior and posterior roots do not anastomose.

Concerning the distribution area of the posterior root, I have only been able to observe that the nerve decussates in the anterior commissure and that the fibres are mingled with the elements of the olfacto-hypothalamic connections.

In lower vertebrates there exist two types of the terminal nerve. It may have two roots, the anterior of which enters the medial hemispheric wall, which also constitutes its distribution area. The posterior root is located outside the hemisphere, and enters the basal parts of the telencephalon medium and distributes over the preoptic nucleus and the hypothalamus. This type exists in certain Selachians (BÄCKSTRÖM, 1924) and Protopterus. In the former, however, both roots may have the same distribution area (Heptanchus, Raja; BÄCKSTRÖM, 1924). In Teleosts (HOLMGREN, 1917, 1920) and Amphibians (MC KIBBEN, 1911) and certain Selachians the other type is developed. This has only one root with its endbranches in the septal formation, nucleus preopticus and hypothalamus. This single root thus corresponds to both the anterior and posterior roots in Dipnoans. In Epiceratodus the conditions show a more or less intermediate stage as the posterior root follows closely the

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olfactory crus with its ganglion situated caudally to the bulbar formation in the vicinity of the ganglion of the anterior root, and with rather well developed connections between the two roots.

Ontogenetically the nervus terminalis in Protopterus develops in immediate contact with the olfactory nerve. In Stage I the nasal placode is connected with the primordium of the forebrain by means of a short nerve, the ventral part of which becoming separated during the development from the dorsal parts, and constitutes the posterior root of the nervus terminalis. The dorsal parts contain the olfactory nerve and the anterior root of terminalis.

According to HERRICK (1937) similar conditions also exist in Urodeles. In early stages of Amblystoma there is only one nerve which connects the nasal placode with the primordium of the olfactory bulb, and this nerve contains direct fibres to the preoptic nucleus. "We may therefore accept Coghill's judgement that in coil to swimming stages, some at least, of the fibres from the nasal epithelium are nervus terminalis". In adult Amphibians also, the terminal nerve is closely allied to the olfactory nerve, while in Dipnoans a portion of the former, the posterior root, becomes separated during the ontogeny from the originally common nervus olfacto-terminalis.

VI. THE PHYLOGENETIC DEVELOPMENT OF THE TELENCEPHALON.

By merely studying the morphology of the telencephalon, one cannot infer any far-reaching conclusions concerning the phylogenetic origin of the dipnoan brain, and one has always to bear in mind that "the evolution of the forebrain in vertebrates is a problem which cannot be solved by the comparative anatomy of the brain of now living animals only as those represent only the upper terminal branches of the great vertebrate stem" (HOLMGREN, 1922). The structure and ontogenetic development of the telencephalon of such an ancient, and in its way of living almost amphibian-like animal as the African lungfish Protopterus may, however, shed some light on the phylogenetic position of the dipnoan brain.

The first investigators paid most attention to external morphological characters, but all of them agree in pointing out the resemblance between the brains of Dipnoans and Amphibians. In two papers (1892 b, 1894) BURCKHARDT has emphasized the fact that the brain of selachians constitutes a primitive type from which the rest of the brains may be derived. "Ehe ich das Selachiengehirn kannte, glaubte ich auch, dass eine Reihe Teleostier-Ganoiden-Dipnoer-Amphibien müsste nachzuweisen sein, bis mir klar wurde, dass das Dipnoergehirn einen zwanglosen Uebergang zwischen dem Selachiergehirn und dem Amphibiengehirn vermittle, nachdem ich die wesentlichen

Kriterien gefunden hatte" (BURCKHARDT, 1892 b; p. 40). According to BURCKHARDT two types originate from the dipnoan brain, one of which gives rise from Epiceratodus via reptiles to the mammalian brain, and the other develops from Protopterus via Gymnophionians into the braintype now existing in Anura and Urodela. STUDNIČKA (1894), however, derives the dipnoan brain direct from the brain of Petromyzon, and he is of the opinion that this fact is evident from BURCKHARDT's investigations. According to BING and BURCKHARDT (1904) one cannot speak of a distinct "Dipnoergehirn". This brain, on the contrary, shows many primitive features which are to be found in both Ganoids and Selachians.

WIEDERSHEIM (1902) points out the great resemblance in brain structures between Dipnoans and Selachians on the one hand, and between the former and the Amphibians on the other. "Ich will damit aber keineswegs eine directe Ableitung von Selachiergehirn befürworten sondern ich bin vielmehr die Meinung dass sich das Selachier- und Dipnoergehirn eines gemeinsames Wurzel entwickelt und sich dann nach zwei verschiedenen Richtungen hin differenziert haben" (p. 226).

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Among later investigators HOLMGREN (1922) especially has tried to connect the different brain types in fishes. Starting from this investigation supplemented by my own observations on the morphology and ontogeny of the dipnoan forebrain, I intend to sum up some of the anatomical conditions in the telencephalon of lungfishes and other lower vertebrates.

Dipnoans-Selachians.

HOLMGREN has pointed out the close agreement in forebrain structure between these two groups. Both have the powerful development of the tuberculum olfactorium, and the nucleus olfactorius lateralis seems to have been built up along fundamentally the same lines, "the apparent difference being caused by the greater differentiation in selachians". Septum also has the same structure with a dorso-rostral and a caudo-ventral part, separated by a sulcus septalis. Pallium seems to be the greatest obstacle in comparing the two brains, but by using an Acanthias-embryo in later stages of development (or other selachians; BÄCKSTRÖM, 1924) it can be proved that the difficulties are not insuperable. "In this embryo the cortex consists of two layers, a distal, where the cells are tangentially stretched, and a ventricular with perpendicular cells. The former corresponds to the cortical layer, the latter to the ventricular in Dipnoi" (HOLMREN, 1922; p. 421). Among lungfishes there is a secondary cortical migration from the ventricular layer as in Selachians. In the latter group, however, this secondary cortex, general pallial cortex, divides the first migrated primordial cortex into a lateral and a medial part. In lungfishes there is no such division, as the general pallial cortex does not reach any degree of

differentiation before it sinks back into the ventricular layer. In the subpallial parts of the dipnoan hemisphere there is also a corresponding reduction of migrated cellparts. The structure of nucleus olfactorius lateralis and tuberculum olfactorium points to the fact that their present, mostly ventricular position, is of a secondary nature. If these brain parts appeared in Dipnoans as migrated formations outside the ventricular layer, the resemblance in the morphology of telencephalon in Dipnoans and Selachians would be still more pronounced.

Dipnoans-Holocephalians.

As in lungfishes, the subpallial parts of the telencephalon in holocephalians are more powerfully developed than the pallial. According to HOLMGREN the pallium is well developed in the rostral half of the hemisphere, but in a caudal direction it "is reduced to a dense cellmass at the upper end of the transversal section. Here the pallium is no longer inverted as it passes over into the pallium-free 'praethalamus' of Edinger" (p. 415)[1]. The same conditions are met with in Dipnoans, where the pallium obviously decreases in size in a caudal direction (cf. figs 29 A—D in this paper).

In Chimaera there exist two cell-layers in pallium. "The distal is not very distinct (figs 24, 25, 27) mostly consisting of scattered cells, sometimes aggregated to form a sort of cell-lamina (fig. 24), sometimes coalescing with the ventricular layer (fig. 26)" (p. 416). I have at my disposal a young specimen cut in transverse sections, stained with Azan-Mallory, and in this it is possible to distinguish a rather well developed pallial cortex in the rostral half of the hemisphere. It is impossible, however, to decide whether this cortex contains a general pallial component.

Concerning the subpallial parts, the conditions remind one of the subpallial structures in the selachian forebrain. The lateral olfactory nucleus and tuberculum olfactorium appear as cortex-like cell-condensations in the external parts of the ventricular cell-layer, but they are not clearly separated from the latter. In the adult form the ventricular layer in both pallium and subpallium has been dissolved and the cells lie diffusedly scattered all over the rather thick hemispheric walls. The above mentioned cell-condensations, however, still exist as indistinct layers in the external parts of these walls.

HOLMGREN (1922) is of the opinion that by removing those structures in the selachian forebrain which are obviously of secondary origin (the pallial and septal fusions between the two hemispheres) we obtain a type of forebrain more or less equivalent to that existing in Holocephalians. In both Dipnoans and Selachians there exist structures which have been developed

[1] "Praethalamus" corresponds to the dorsal parts of the telencephalon medium (pars superior of nucleus preopticus) in Protopterus, which as in Holocephalians is intercalated between pallium and the diencephalic centers.

in the same manner in both groups, and the Holocephalians therefore show structures similar to those met with in the dipnoan forebrain. It must be pointed out, however, that the lack of embryological material of Holocephalians makes a comparision as yet rather uncertain.

Dipnoans-Actinopterygians.

By having an exverted telencephalon, Polypterus, Chalamoichtys, all Ganoids and Teleosts differ from the architectural plan typical of the lungfishes. The telencephalic centres are almost completely migrated and the ventricular cell-layer, therefore, is very thin. The migrated cells may be arranged in several thin strands outside one another (Osmerus, HOLMGREN, 1920; Acipenser, JOHNSTON, 1911 a, fig. 49), but no cortical structures exist analogous to those in Selachians and Dipnoans. HOLMGREN (1922) is of the opinion that the exverted brain may have developed from an inverted braintype and HOLMGREN and VAN DER HORST (1925) show that there exists in Polypterus, Amia and some Teleosts a small evaginated part behind the bulbus ventricle, which contains a rudimentary septum. Because of this the authors point out that "The form series treated with above seem to show that the forebrain of teleosts is principally evaginated and has to be derived from a type where the pallial part of the medial wall is epithelial (devoid of nervous tissue) as is the case in Ceratodus" (p. 82).

In comparing KAPPERS' figs 1 and 2; Tafl. 18 (1907) with HOLMGREN and VAN DER HORST's figs 3 and 4, one finds considerable resemblance in the rostral parts between the forebrains of Amia and Epiceratodus. In Epiceratodus there also exists a slight bending upwards of the mesial part of the pallium where the dorsal border of the ependymatic membrane (lingula interolfactoria) is attatched. If the ependymatic septal wall in Amia had a more caudal extension and the basal parts of telencephalon were deepened in a ventro-lateral direction we should get a telencephalon which, except for the rather heavy exversion, would be almost of the same build as that of the Epiceratodus. Since parts of the medial wall are ependymatic, no fibre connections pass between pallium and septum in this wall in Epiceratodus. These connections lie in the lateral wall, and pass round the basal parts of the hemisphere and then up to septum, which builds up the ventral, nervous part of the medial wall. The same conditions exist in Protopterus even though no ependymatic part of the medial wall exists in the adult animal. The fibre tracts between the pallium and the septal parts in the dipnoan hemisphere have thus the same position as in exverted brains.

From the comparisons made above it is evident that the dipnoan forebrain contains structures which are specific for different groups of fishes, and it

seems to me, therefore, that this brain must be rather closely related to the brain type which has been the starting point for both the exverted and the inverted brain-types.

Dipnoans-Amphibians.

The structure of the telencephalon in the adult brains of lungfishes and Amphibians presents some common traits. They have fully developed, evaginated and perfectly separated hemispheres, and the ventricular position of the cell-areas is characteristic of both groups. The morphological structure also of these areas have much in common. But differences nevertheless occur. In Dipnoans the septal formation and the basal parts of the hemisphere are considerably more developed than in the Amphibia. In the latter group the medial parts of the pallium are very pronounced, but pallium lacks the cortical formation which is such an outstanding feature of the dipnoan forebrain. There is a trace of a "cortex olfactoria" in tuberculum olfactorium in Anura, but in Urodela there is no such formation (SÖDERBERG, 1922).

A comparison of the ontogenetic development of telencephalon in Dipnoans and Amphibians, however, gives quite a different picture. Among lower vertebrates now living we have no other group than the Amphibia which has so many traits in common with dipnoan forebrain-ontogeny. In very early embryonic stages the primitive forebrain is bent downwards in a ventral direction. This bending down is very little pronounced in Anura, but in lungfishes and in Urodela it is well marked. The hemispheric evagination begins in the dorso-caudal parts of the telencephalic primordium, that is, in the pallium. In both Amphibians and Dipnoans this part produces a caudal lobe, dorsally and caudally to the foramen Monroi, and on the medial side the lobe is attatched to the rostral parts of the diencephalon by means of a "massa cellularis reuniens". The early ontogenetic development of the telencephalon medium and the commissural ridges has a similar course, and in both groups we have in embryonic stages a septum ependymale, which in lungfishes and Urodeles gives rise to diverticles which in the adult brains build up the lateral choroidal plexa. In addition we have the ontogenetic development of the tuberculum olfactorium and the nucleus olfactorius lateralis of the two groups and the presence of an embryonic pallial cortex in Amphibia as well.

In the anuran subpallium we have cell-areas which are homologous to similar areas in reptiles (HERRICK, 1921 b; SÖDERBERG, 1922). According to HERRICK (1927, 1933 a) there exist in the subpallium of Urodela certain cell-areas (strio-amygdaloid complex) which are characteristic of higher vertebrates. In Amblystoma they seem to be a little more differentiated, but in other urodeles they are not clearly differentiated from other parts of the ventricular cell-layer, and they have to be considered as more or less undifferentiated primordia. Such primordia, however, already exist in lungfishes.

The morphology and the ontogenetic development of telencephalon in lungfishes and Amphibians have so many things in common that there is reason to believe that the amphibian forebrain has originated from a braintype which may have been closely related to that existing in primitive Dipnoans. This is especially the case in the Urodela. The Anura differs somewhat from the latter. The "Kopfbeuge" is very little pronounced, and the ependymatic part of the septal wall very soon disappears, in marked contrast to the conditions in Dipnoans and Urodeles. The different forebrain nuclei are much more differentiated in Anura, and SÖDERBERG (1922) remarks that "In the Anura the ontogenetic appearance of the transitory nuclei is more clearly manifested than in the urodeles. From this fact the conclusion may be drawn that the anuran forebrain corresponds more clearly to that of the stegocephalians than to that of the urodeles. These two groups may have followed different lines of development. In the urodeles reduction of the forebrain nuclei may have taken place at an earlier period than in the Anura, in consequence of the differentiation of the transitory nuclei being less pronounced" (p. 118).

JOHNSTON (1910, 1923) is of the opinion that in forebrain phylogeni we have two lines of development, the one represented by Ganoids-Teleosts-Amphibians and the other by Selachians-Reptiles-Mammals. In the latter branch he includes the lungfishes. In his opinion the telencephalic commissures are decisive. "The fact that the hippocampal commissure crosses beneath the ventricle shows the affiliation of the amphibians with primitive ganoid-like ancestors.... It is unfortunate that we have not a more complete account of the telencephalon of dipnoans, but enough is known (Kerr, Smith, Holmgren) to show that they possess a true dorsal pallium and commissures comparable with the hippocampal formation of reptiles" (1923, p. 173). In JOHNSTON's 1910 paper he points out that in Selachians-Reptiles-Mammals the commissura hippocampi is placed in lamina supraneuroporica, whereas in Ganoids-Teleosts-Amphibians it is placed in lamina terminalis.

In Dipnoans there is no distinct recessus neuroporicus and it is very difficult, therefore, to determine exactly the border between lamina supraneuroporica and lamina terminalis. When commissural fibres begin to appear they are all in the ridge of the future commissura anterior, which during the whole ontogenetic development is situated in the ventro-caudal parts of the lamina terminalis. Even in very late, almost adult stages, in both Protopterus and Epiceratodus none of the commissural fibres are situated outside the by this time very sharply defined commissural ridge. In the fullgrown animal the ridge has been stretched out in a dorsal direction and all fibres in this dorsal part belong to the septal formation. As there is no extension downwards of pallial fibres into the septal wall, the hippocampal commissure cannot be placed in the dorsal part of the comissural ridge nearest to the part of the anterior wall containing the region in which lamina supra-neuroporica and

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lamina terminalis meet. The commissura hippocampi cannot, therefore, be in lamina supra-neuroporica. Instead, pallial commissural fibres are found in the caudal part of the ridge of the anterior commissure, which is in exactly the same position as in Amphibians, that is, in the lamina terminalis.

JARVIK (1942) in his work on the snout of Crossopterygia hos pointed out that Urodela must be closely related to the Porolepiformes among the Crossopterygia. The former, however, are not related to the Dipnoi. "As far as I can see there is nothing in the snout to support the belief that the Porolepiformes and Dipnoans are closely related to each other" (p. 392)[1]. To support his view concerning the origin of the Urodela, Jarvik also uses the morphology of the brain in Urodeles and Porolepis. According to him the latter must have had a rather curious brain (see fig. 38, p. 363) with the olfactory nerve inserted far caudally in the ventro-posterior part of the telencephalon. This condition Jarvik compares with the embryonic brain in Urodela. "It is of great interest to find, therefore, that in the larvae of Urodeles the bulbus olfactorius lies further posteriorly in relation to the anterior end of the hemisphere than in the adults.... This condition is obviously due to the position of the hemispheres in the larvae. In the larvae these divisions of the forebrain extend far forwards between the nasal sacs quite as they must have done in Porolepis, but are then completely or almost completely retracted from the ethmoidal region" (p. 396).

It seems to me almost impossible to get any clear conception of the shape of extinct brains only on a basis of the cast of the endocranial cavity[2]. We do not know whether the part of this cavity which lies in front of the point of insertion of the nervus olfactorius really contained any brainparts. The forebrain of Porolepis may have been very short, or it may, as Jarvik himself has pointed out, have resembled the selachian forebrain in having a laterally inserted olfactory nerve (see JARVIK p. 384 and his fig. 45). But even if Jarviks conception of the brain of Porolepis represents the real conditions, it does not tend to connect the Porolepiformes more closely to the Urodela than for instance to the Dipnoans. In the latter we have in larval stages the same caudo-ventral position of the olfactory nerves, which can be clearly seen from the ontogenetic development. Thus I do not think that the data concerning the forebrains set forth by Jarvik has any bearing upon the problem of the origin of the Urodela.

[1] SÄVE-SÖDERBERG (1934), however, is of the opinion that the Dipnoans are closely related with the Urodeles among the Amphibia. See also ROMER (1937) who has tried to restore the brain of a Crossopterygian (Uregalichthys) and who points out that "It is obvious that the brain as restored is essentially similar to that seen in dipnoans on the one hand and amphibians on the other; thus the neurological evidence, as far as it goes, agrees with all other lines of work tending to indicate the close relationship of crossopterygians with these two groups" (p. 34).

[2] See EDINGER (1929) who discusses the relation between brain and cranial cavity in recent and extinct forms (pp. 30—32).

Different types of forebrains and their probable relationship.

As there seems to be little hope of getting any accurate data on the crossopterygian brain by investigating the extinct forms only, we have to deduce some facts from the conditions in the brains of those recent lower vertebrates which seem more or less to have had some connections with this stem-group. A comparison of the brains of different gnathostome vertebrates shows that there exist three more or less well defined types of forebrains and these are:

A. Forebrains with evaginated, more or less inverted hemispheres, with a rather well developed ventricular cell-layer and cell-areas differentiated from this which, if they are quite free from the ventricular layer, appear in the form of migrated cortices both in pallium and subpallium. This type exists in Selachians, Holocephalians, Dipnoans and Amphibians. It is typically developed in older embryos of Selachians. In the other groups the migrated cell-areas both in pallium and subpallium show an increased tendency to sink back into the ventricular layer. This reduction has gone furthest in Amphibians, were there are no migrated parts in the subpallium, and the pallial cortex only appears in early ontogenetic stages.

B. Forebrains with evaginated and inverted hemispheres with migrated cell-areas which, unlike type A, become more and more differentiated and develop into complicated nuclear groups. This type of forebrain exists in Sauropsida and Mammalia.

C. Forebrains with exverted lateral walls. The ventricular cell-layer is very thin. Migrated cell-areas both in pallium and subpallium which, however, do not form typical cortices. No paired hemispheres except for a small anterior rudiment comprising the region of the olfactory bulb. Polypterids, Ganoids, Teleosts.

As has already been pointed out, the dipnoan forebrain shows structures characteristic of both A and C, and this seems to indicate that these two types may have developed out of a common brain-type which may have been built up somewhat similarly to that existing in older embryonic stages of Dipnoans. In some structures it was probably more differentiated as the dipnoan forebrain seems partly to have been subjected to a reduction.

Such a common ancestral forebrain-type has already been described by HOLMGREN (1922). He has reconstructed a brain which in his opinion was common to the ancestors of Selachians, Holocephalians and primitive Crossopterygians. This forebrain was probably evaginated (see also HOLMGREN and VAN DER HORST, 1925, pp. 81—82), inverted and with a pallium which contained two cell-layers, a cortical and a ventricular. "Further it is probable that the pallium was already subdivided into the typical three parts, the

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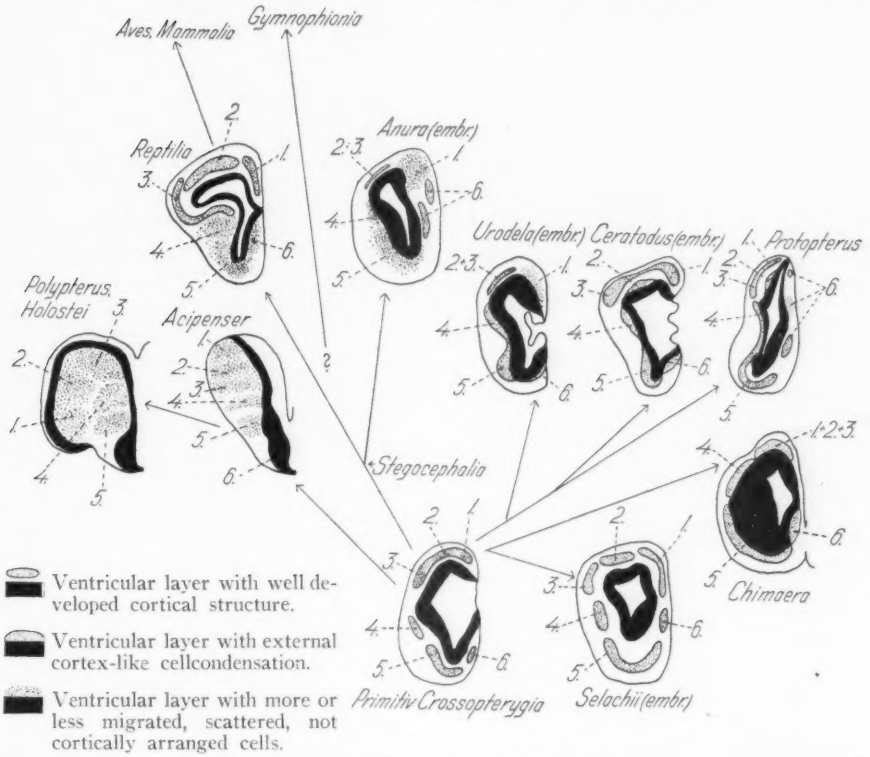

Fig. 47. Schematic drawing showing different types of forebrain in lower vertebrates and their probable relationship.
1. Hippocampus; 2. general pallium; 3. pyriformis; 4. nucleus olfactorius lateralis; 5. tuberculum olfactorium; 6. septal nuclei.

hippocampal, the general, and the pyriforme pallium. This is a conclusion drawn from the fact that in Polypterids, Ganoids and Teleosts the subdivided pallium is the rule. But also in Dipnoi there are signs of a subdivided pallium. Also in the parallel group of selachians a similar subdivision is present, at least in the embryo" (HOLMGREN, 1922, p. 436). HOLMGREN also is of the opinion that in the subpallium there existed differentiated cell-areas. "Therefore I am disposed to believe that the primitive crossopterygians had a tuberculum olfactorium removed from the ventricular wall" (p. 438). In some of the primitive crossopterygians a part of the medial wall may have been epithelial and devoid of nervous tissue, and at the same time showing a tendency to press out the dorsal parts of the lateral wall, as for instance is the case in the adult forebrain of Epiceratodus. If the conditions were favourable (see KAPPERS, 1908) this rudimentary exversion may have been more and more accentuated. The ependymatic parts of the mesial wall must then have been considerable stretched and in the ventral parts fused with the same

structure in the other hemisphere. Finally this stretching caused a separation of the dorsal and ventral parts of the fused portion. This process may be illustrated by a serie of transverse sections through the anterior parts of the forebrain of Amia (KAPPERS, 1907; figs 1—3, Talf. 18). I have tried to illustrate in fig. 47 the hypotetical relationship between different types of forebrains in vertebrates.

As has already been mentioned there exist differences between the forebrains of Anura and Urodela. In the pallial formation these differences are not apparent. In adult Anura no pallial cortex exists, but as SÖDERBERG has shown larval stages show a cortical delamination which later sinks back into the ventricular layer exactly as in the Urodela. In the subpallial parts, however, the conditions are different in the two groups. In larval Urodela the nucleus olfactorius lateralis together with the tuberculum olfactorium constitutes a common, in a lateral direction concave, and in the ventral part almost cortex-like, cell-condensation in the external parts of the ventricular layer as in Dipnoans, whereas in larval Anura the gray matter in the ventro-lateral part of the hemisphere is built up of separated cell-areas, conditions which according to SÖDERBERG are reptilian in character. In my material older embryos of Bufo and Xenopus clearly show a marked tendency to form cell-areas in the fibre layers outside the rather thin ventricular layer in the ventro-lateral part of the hemispheres.

From the above mentioned facts it appears as if the anuran forebrain belongs to group B, but some parts of this brain, i.e. the pallial cortices, have been subjected to a reduction analogous to the conditions in the Dipnoans and Urodeles. The differences in telencephalic morphology in Anura and Urodela pointed out above and on p. 142 are naturally not sufficient to infer that the two groups have a different phylogenetic history. In other brainparts however, there is also an obvious difference between the two amphibian groups. Thus the anuran mesencephalon is built up in a way that reminds one of reptilian condition with alternating layers of gray and white matter, a structure which differs distinctly from the primitive conditions in Urodela which in this brainpart do not show any fundamental differences from the Dipnoans (see also KAPPERS, HUBER, CROSSBY, 1936; pp. 942—944).

Investigations on other morphological units show that there exists a difference between the Anura and the Urodela, a difference sufficiently great to make the authors inclined to doubt the phylogenetic affinity between the two groups. WINTREBERT (1910, 1922) in studying the cranial bones in Amphibia remarks that there is a marked difference between the Urodela on the one side and the Anura and Stegocephalia on the other, and he is of the opinion that the Urodela show a closer relationship to the Dipnoi.

HOLMGREN (1933) who studied the origin of the tetrapod limb is of the opinion that the Anura together with the Stegocephalians and higher verte-

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brates have developed out of fishes "with dichotomically branched pectoral fin skeleton, whereas the urodeles must be considered to have originated from fish ancestors (crossopterygian or dipnoan), with a short biserially arranged archipterygium" and further on he remarks that "regarding the limbs there is a greater agreement between a dipnoan and an urodele, than between an urodele and an anuran" (p. 288). KERR (1932) has pointed out the great resemblance between Amphibians and Dipnoans, and he states "There is another feature which would be by itself almost convincing to anyone experienced in Dipnoan study, namely the general agreement in histological structure of the tissues with those of the Urodele Amphibia" (1932, p. 421). HERRE (1935) has investigated recent and extinct urodeles and is of the opinion that "Auf Grund der anatomischen, biologischen und palaeontologischen Befunde kommen wir also zu dem Schluss, dass die Ordnung der Urodelen, der Anuren und wohl auch der Gymnophionen und der Stegocephalen unabhängig von einander aus Fischformen hervorgegangen sind; somit für die Klasse der Amphibien eine polyphyletische Entwicklung in sehr hohem Grade wahrscheinlich" (p. 70). KINDAHL (1937) is of the opinion that the structure of the urogenital system speaks in favour of a closer affinity between Urodeles and Dipnoans, and that the Anura and Gymnophionia "im Hinblick auf diese Organe anderen Ursprungs zu sein scheinen". JARVIK (1942), also on a basis of the conditions in the snout states that the Urodela and Anura have a different phylogenetic origin.

WICKBOM (1944) who made cytological studies in Dipnoi and Amphibia is of the opinion that there is "a closer relationship between Urodela and Dipnoi than between Anura and either of the other two groups".

The differences in the morphology and the ontogenetic development of the telencephalon in Anura and Urodela, together with the results of the authors mentioned above, seem to argue in favour of a different phylogenetic origin of the two groups. In any case the conditions clearly show a resemblance between urodelean and dipnoan forebrain organisation, a resemblance great enough to indicate a genetic relationship between these two groups.

In comparison with the Anura and the Urodela we have a rather scant knowledge of the gymnophionian brain. The earlier investigators (WIEDERSHEIM 1886, WALDSCHMIDT 1887, SARASIN 1890, BURCKHARDT 1891) have pointed out those more obvious structures in which the Gymnophionia differ from other Amphibians. Among these structures is the rather enormous development of the caudal parts of the hemispheres, with the caudal lobe on the same level as the foremost parts of the myelencephalon. In the caudoventral parts of the hemisphere there exists a well developed "lobus temporale" (SARASIN), a structure to which we apparently have no parallel among other lower vertebrates. According to a more recent investigation of KUHLENBECK (1922 b) there exists in pallium, outside and clearly separated from the ven-

tricular layer in the adult forebrain, a "Schwärmschicht" containing well developed "Pyramidenzellen". This "cortex", however, is not so well developed as in Dipnoi, but more accentuated than in Anura and Urodela. It is more distinct in the medial parts. Nucleus olfactorius lateralis (Epistriatum, KUHLENBECK) is representated by a thin undifferentiated ventricular layer, which reminds one of the same structure in Urodela and Epiceratodus. The ventro-lateral part of the hemispheres is built up by a rather thin undifferentiated ventricular cell-layer (Nucleus basalis) and outside this there exists a cortex olfactoria. This begins in the frontal parts of the hemisphere as "eine sehr lockere Schwärmschicht dem Nucleus basalis aufliegt, bald aber sich gänzlich von diesen ablöst und als selbständige Rindenplatte an die ventrolaterale Hemisphärenfläche rückt" (p. 473). A similar structure exists in Protopterus where, however, the cells of the cortex olfactoria are much more densely arranged in contrast to the more diffuse appearance of the same structure in Gymnophionians. According to KUHLENBECK there also exists in lobus temporalis a cortex-like "Schwärmschicht". This area ventrolateralis of KUHLENBECK reminds one somewhat of the caudal lobe in the hemisphere of the adult forebrain of Protopterus, which contains the caudal parts of the cortex olfactoria. There exists a difference, however, as there does not seems to be any direct continuation between this cortex-like formation in lobus temporalis and cortex olfactoria, as is the case in Protopterus. KUHLENBECK points out that the septal nuclei in Gymnophionia has the same structure as in Urodela, but concerning the septum there seems to me that a comparison with the Anura is more easily found. In both groups the mesial hemispheric wall is very thick and protrudes into the lateral ventricle. There exists a distinct zona limitans medialis and well developed septal nuclei. As in the Anura there is no septum ependymale.

The gymnophionian forebrain shows, therefore, structures which are to be found in Anura, Urodela and Dipnoans, and according to KUHLENBECK also in Reptilia. This forebrain, therefore, may belong either to group A or B. Unfortunately there is no data concerning the ontogenetic development of this brain except for a paper by LAUBMAN (1927) on Hypogeophis, but this investigation concerns mostly the outer morphology and does not treat the telencephalic cell-areas and their development. My own material consists of some older embryos of Ichtyophis, which in some points differ from the description of KUHLENBECK (1922 b). His material consisted of adult specimens of Ichtyophis, Hypogeophis, Siphonops and Cryptosophis ("wahrscheinlich"). In my specimens there is no trace of a pallial cortex and if such a cortex exist in the fullgrown animal as KUHLENBECK points out, this must have been differentiated from the ventricular layer very late in the ontogenetic development. This argues against a closer relationship with type A where we have in ontogenetic stages found a trace of a more or less well developed

pallial cortex which has been subjected to a reduction. For lack of a detailed ontogenetic investigation, however, it is impossible to decide whether there has been a reduction of a more differentiated forebrain as in Anura, Urodela and Dipnoans, or whether the Gymnophionian forebrain is related to a type which must have been the forerunner to the more highly differentiated forebrain in reptiles (type B).

VII. SUMMARY.

1. The Dipnoan forebrain develops out of two transversally extended proliferation zones in the anterior part of the primitive forebrain. The rostral zone gives rise around its proliferation groove, sulcus subpallialis, to nucleus olfactorius lateralis, tuberculum olfactorium and the septal formation. The caudal zone gives rise around sulcus intraencephalicus anterior to pallium and nucleus preopticus. Bulbus olfactorius develops out of the subpallial zone but probably contains elements (accessory olfactory bulb) pallial of origin.

2. The hemispheric evagination starts in the dorsal part of the caudal zone (pallial primordium).

3. The ontogenetic development of telencephalon is principally the same in Monopneumonia, Dipneumonia and Urodela, and not until in rather late embryonic stages do the structures develop which are characteristic of the adult brains of these three groups.

4. Pallium has a well developed primordial cortex. Traces of a general pallium cortex rudiment exist.

5. The caudal parts of the lateral olfactory nucleus contain structures which correspond to the ventro-lateral nucleus of Urodeles (primordium of corpus striatum).

6. Tuberculum olfactorium is powerfully developed with a conspicuous cortex. The conditions indicate that this cortex must previously have had a greater extension.

7. The septal formation builds up the part of the medial hemispheric wall which contains nervous tissue. Both nucleus lateralis and medialis septi are present. The latter consists of two parts separated from each other, the dorsal of which corresponds to the pars precommissuralis of nucleus olfactorius anterior in Actinopterygians. The ventral part corresponds to the caudal part of the medial septal nucleus in Selachians and Amphibians. The septal wall contains an epithelial structure (septum ependymale) which develops into the choridal plexa of the hemispheric ventricles.

8. Nucleus preopticus constitutes the telencephalon medium, the dorsal part of which (pars superior of nucleus preopticus) corresponds to area

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somatica in fishes and probably to the strio-amygdaloid complex in Urodeles. Nucleus magnocellularis is present.

9. Nervus terminalis in Protopterus has an anterior and a posterior root as in Epiceratodus.

10. In recent gnathostom vertebrates there exist three types of forebrain which seem to have originated from a common brain-type. The Dipnoan forebrain, together with that of Selachians, Holocephalians and Amphibians, belongs to a type which in some species has been subjected during the development to a reduction of migrated (cortical) cell-areas. In these typological series the forebrains of Dipnoans and Urodeles seem on account of the morphological structure and ontogenetic development to have the closest phylogenetic connection.

VIII. LIST OF LETTERINGS.

a.v., angulus ventralis in the lateral ventricle.
bl.v., blood vessel.
b.olf., bulbus olfactorius.
bulb.prim., primordium of bulbus olfactorius.
b.v., ventricle in bulbus olfactorius.
c.a., commissura anterior.
c.a.r., ridge of the anterior commissure.
c.c., cell-clusters outside the tuberculum olfactorium.
ch., chiasma.
ch.r., ridge of the chiasma.
c.h., commissura hippocampi.
c.hab., commissura habenularis.
c.i.b., commissura interbulbaris.
c.p., commissura posterior.
c.s., commissura septi.
d.B., diagonal band of Broca.
d.gr.c., dendrite of granular cell.
d.s.c.c., dendrite of supracortical cell.
d.t.r., di-telencephalic ridge.
ep., epiphysis.
f.M., foramen Monroi.
fov.limb., fovea limbica.
g.h., ganglion habenulae.
gl., glomerulus in bulbus olfactorius.
g.N.t.a., ganglion of nervus terminalis anterior.
g.p.c., general pallial cortex.
gr.c.l., granular cell-layer in bulbus olfactorius.
h., hemispheric primordium.
h.c., hippocampal cortex.
h.v., hemispheric ventricle.
hyp., hypothalamus.
i.g.c., interglomerular cell.
l.f.b., lateral forebrain bundle.
l.p., lateral prominentia of cells in bulbus olfactorius.
m.c., mitral cells.
m.c.l., mitral cell-layer.
m.c.r., massa cellularis reuniens.
m.f.b., medial forebrain bundle.
n.c.a., nucleus of anterior commissure.
n.i.g.c., neurite of interglomerular cell.
n.l.s., nucleus lateralis septi.
n.m.c., nucleus magnocellularis.
n.m.s., nucleus medialis septi.
n.m.s.d., dorsal part of nucleus medialis septi.
n.m.s.v., ventral part of nucleus medialis septi.
N.olf., nervus olfactorius.
n.olf.l., nucleus olfactorius lateralis.
n.olf.l.p.d., nucleus olfactorius lateralis pars dorsalis.
n.olf.l.p.v., nucleus olfactorius lateralis pars ventralis
N.opt., nervus opticus.
n.po., nucleus postopticus.
n.pr., nucleus preopticus.
n.pr.p.i., nucleus preopticus pars inferior.
n.pr.prim., primordium of nucleus preopticus.
n.pr.p.s., nucleus preopticus pars superior.
n.t., nucleus taeniae

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N.t., nervus terminalis.
N.t.a., nervus terminalis anterior.
N.t.p., nervus terminalis posterior.
n.v.th., nucleus ventralis thalami.
olf.f., fila olfactoria.
p.a., anterior pole of the hemisphere.
pall., pallium.
pall.prim., primordium of pallium.
pall.c., pallial cortex.
par., paraphysis.
p.c., cortex pyriforme.
p.c.c., cell from pallial cortex.
p.c.n.o.a., nucleus olfactorius pars precommissuralis.
p.c.th., pars caudalis thalami.
p.d.s., pars dorsalis septi.
p.fr.th., pars frontalis thalami.
p.f.s., pars fimbrialis septi.
pl.ch.d., plexus choroideus dorsalis.
pl.ch.l., plexus choroideus lateralis.
pl.ch.v., plexus choroideus ventralis.
pl.ch.III., plexus choroideus in third ventricle.
pl.v., plica encephali ventralis.
p.m.th., pars medialis thalami.
p.t.p., pars tuberculi posterioris.
p.v.s., pars ventralis septi.
r.opt.l., recessus opticus lateralis.
r.po., recessus postopticus.
r.pr, recessus preopticus.
sacc.d., saccus dorsalis.
s.c.c., supracortical cell.
s.d.d., sulcus diencephalicus dorsalis.
s.d.m., sulcus diencephalicus medialis.
s.d.t., sulcus di-telencephalicus.
s.d.v., sulcus diencephalicus ventralis.
s.em.th., sulcus eminenthiae thalami.
s.ep., septum ependymale.
sept., septum.
s.h., sulcus hypothalamicus.
s.i.a., sulcus intraencephalicus anterior.
s.l.b.e., sulcus limitans bulbi externus.
s.l.b.i., sulcus limitans bulbi internus.
s.l.h., sulcus limitans hippocampi.
s.l.l., sulcus limitans lateralis.
s.l.p.l., sulcus limitans pallii lateralis.
s.p., sulcus pallialis.
s.pr., sulcus preopticus.
sp.prim., subpallial primordium.
s.s., sulcus septalis.
s.sp., sulcus subpallialis.
s.sp.d., sulcus subpallialis dorsalis.
s.t.p., sulcus tuberculi posterioris.
str.am.c., strio-amygdaloid complex.
str.m., stria medullaris.
sub.pl., subependymal plexus.
term.r., terminal ridge.
Tr.c.h., tractus cortico-habenularis.
Tr.c.t., tractus cortico-tegmentalis.
Tr.olf.d.l., tractus olfactorius dorso-lateralis.
Tr.olf.e., tractus olfactorius externus.
Tr.olf.h.l., tractus olfacto-habenularis lateralis.
Tr.olf.h.v., tractus olfacto-habenularis ventralis.
Tr.olf.hyp.l., tractus olfacto-hypothalamicus lateralis.
Tr.olf.hyp.m., tractus olfacto-hypothalamicus medialis.
Tr.olf.hyp.v., tractus olfacto-hypothalamicus ventralis.
Tr.olf.m., tractus olfactorius medialis.
Tr.olf.v., tractus olfactorius ventralis.
Tr.olf.v.l., tractus olfacto-ventrolateralis.
Tr.olf.v.l.m., tractus olfacto-ventrolateralis medialis.
Tr.pall., tractus pallii.
Tr.pr.h., tractus preoptico-habenularis.
Tr.s.h., tractus septo-habenularis.
Tr.str.hyp., tractus strio-hypothalamicus.
Tr.str.t., tractus strio-tegmentalis.
Tr.t., tractus taeniae.
tub.olf., tuberculum olfactorium.
tub.olf.c., cortex of the tuberculum olfactorium.
tub.olf.p.a., tuberculum olfactorium pars anterior.
tub.olf.p.p., tuberculum olfactorium pars posterior.
v.c.c., ventricular cortical cell in pallium.
v.c.l., ventro-caudal lobe in the hemisphere.
v.f.b., ventral forebrain bundle.
v.m.c., ventro-medial cells in tuberculum olfactorium.
v.p.c., cell from ventricular layer in pallium.
v.t., velum transversum.
z.l.l., zona limitans lateralis.

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SOME PROBLEMS CONCERNING THE DEVELOPMENT OF THE SKULL OF TURTLES

BY

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(With 18 figures in the text)

Although the general outlines of the development of the skull of turtles are comparatively well known, through the fundamental descriptions by RATHKE (1848), and PARKER (1880), followed by more recent investigations made by, for instance, NICK (1912) on Dermochelys, and SHANER (1926) on Chrysemys, there are still various problems under discussion, or left unsettled for future research. One reason for the difference of opinion amongst later investigators, is, no doubt, the lack of well-preserved specimens of sufficiently young embryonic stages suitable for examination on complete series of microscopic slides.

I have had the opportunity of examining several embryonic stages of the rare Chelonian Dermochelys coriacea, from the collections of the Zootomical Institute of Stockholms Högskola, placed at my disposal by the head of the Institute, professor NILS HOLMGREN. It is a great pleasure to me to express my gratitude to professor Holmgren for this generous offer. The value of the Dermochelys material is greatly increased by the existence, in the rich collections of embryonic material of the Zootomical Institute, of a fairly complete series of embryonic stages of the Cheloniid Lepidochelys olivacea, as well as of various embryonic specimens of other reptiles, including some stages of Chrysemys.

As working through the whole material will be a rather comprehensive task, I have preferred to limit the scope of this paper to an attempt at settling two problems which present themselves as comparatively independent of the rest. They are the parasphenoid-problem, and the question of the intertrabecular (taenia intertrabecularis).

The material for dealing with these two problems comprises four embryonic stages of Dermochelys, respectively 17, 19, 21 and 29 days old, a series of Lepidochelys at the age of 14, 15, 16, 17, 18, 19, 20, 21, 22, 23, 24, 26 and 28 days old respectively, and some embryonic stages of Chrysemys marginata.

THE PARASPHENOID.

The parasphenoid in Chelonians was, for a long time, supposed to be lacking, and the oblong ventral bone disc visible for instance in Dermochelys anteriorly to the occipital was interpreted as part of the basisphenoid. Not until 1905 GAUPP described the parasphenoid in embryos of Podocnemis as a separate, ossified dermal element, forming the bottom of the sella, and the anterior end of the basisphenoid. In the adult it fuses partly with this bone, together with which it forms the parabasal canals for the carotids. According to GAUPP there was great resemblance between this Chelonian parasphenoid, and the T-shaped parasphenoid of the Saurians.

VERSLUYS (1906) discovered that what had been interpreted as the ventral portion of the so-called basisphenoid in adult specimens of Dermochelys is really a large parasphenoid, partly because it overlaps the pterygoids from underneath, a position impossible for a primordial bone, partly because of the shape and position of the rostrum which is situated where the crus longitudinale of the parasphenoid lies in Saurians and Rhynchocephalians.

Later (1910), FUCHS discovered the parasphenoid in Emys as a small flat bone underneath the hypophysis, but in no way resembling the parasphenoid in Saurians. According to him it corresponds to a portion of the longitudinal part of the Saurian parasphenoid, whereas there is no portion homologous to the crus transversum. The existence of a parasphenoid in Emys was confirmed by KUNKEL (1912). Further, FUCHS stated after having examined embryonic, as well as adult specimens of Chelone imbricata, that a parasphenoid is entirely missing in that species, even as a rudiment during the ontogeny. Thus, the well developed basisphenoid rostrum in adult specimens of Chelone cannot be interpreted as anything but an ossification in the primordial skull, i.e. the true basisphenoid.

From the conditions in Chelone, FUCHS concluded, concerning Dermochelys —a species he had not examined — that VERSLUYS could not have been correct in his opinion as to the existence of a parasphenoid in that turtle.

The definite answer to the question of the existence of a parasphenoid in Dermochelys was given by NICK (1912). He had at his disposal not only several skulls of adult specimens of Dermochelys, but also two "ripe" embryos, ready to hatch. He confirmed VERSLUYS's opinion concerning the parasphenoid.

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The conclusive argument is founded on his examination of the embryos where the rostrum of the parasphenoid was situated under the ossified intertrabecle from which it was plainly separated by means of a suture. In the region of the dorsum sellae the parasphenoid was fused with the periost of the basal plate and thus difficult to demarcate, but behind that portion it was again well isolated from the cartilage of the base of the skull. Posteriorly it tapered, and ended on the level of the fenestra ovalis, which corresponds to the extension caudad of the basisphenoid of the adult.

As to Chelonia, NICK who had examined two "ripe" embryos confirmed FUCH's statement that no trace of a parasphenoid was to be found under the basal plate. He could not deny, however, the possibility that the ossified lamellae, ventrally to the intertrabecle, might partly correspond to a parasphenoid, and be identified as such at a suitable stage.

Also in Chelydra NICK had found the parasphenoid. In a ripe embryo the fossa hypophyseos was closed ventrally by the anterior end of the parasphenoid. In that part the bone was entirely separated from the basis cranii. Such was the case also where the carotids entered the cavum cranii. Further back it was intimately fused with the basal plate, and in front of that region with the perichondrial ossifications of the trabecles. In adult specimens of Chelydra the parasphenoid had fused with the basisphenoid, to form one single bone, but the parasphenoidal rostrum was still recognisable. In Chelydra but not in Dermochelys the pterygoids were to a great extent overlapped by ossified lamellae, probably, according to NICK, derived from the parasphenoid.

My own investigations show also that there is no doubt that a parasphenoid is developed in Dermochelys in the place indicated by NICK. In the oldest of the embryos at my disposal, the 29 days specimen, with a carapace length of 13.5 mm, all dermal bones are already developed whereas hardly any signs of beginning perichondrial ossification show. The parasphenoid (fig. 1) is a comparatively short bone plate. In shape and size it resembles the parasphenoid described by KUNKEL in his 13.5 mm (carapace length) embryo of Emys. It is almost triangular, with the blunt point directed forward. The base has a deep and irregular indentation. It shows all the characteristics of a dermal bone, and is separated everywhere from the cartilage of the primordial skull by a stratum of mesenchymatous tissue, but the position is not exactly the same. While the bone in KUNKEL's embryo is situated under the fenestra hypophyseos, with the median process extending as far forward as the anterior margin of the fenestra, and the postero-lateral processes just reaching its lateral margins, the bone in the Dermochelys embryo is situated entirely behind the fenestra, and is larger in comparison with it. In NICK's ripe embryos the parasphenoid is still larger, especially longitudinally. The anterior end

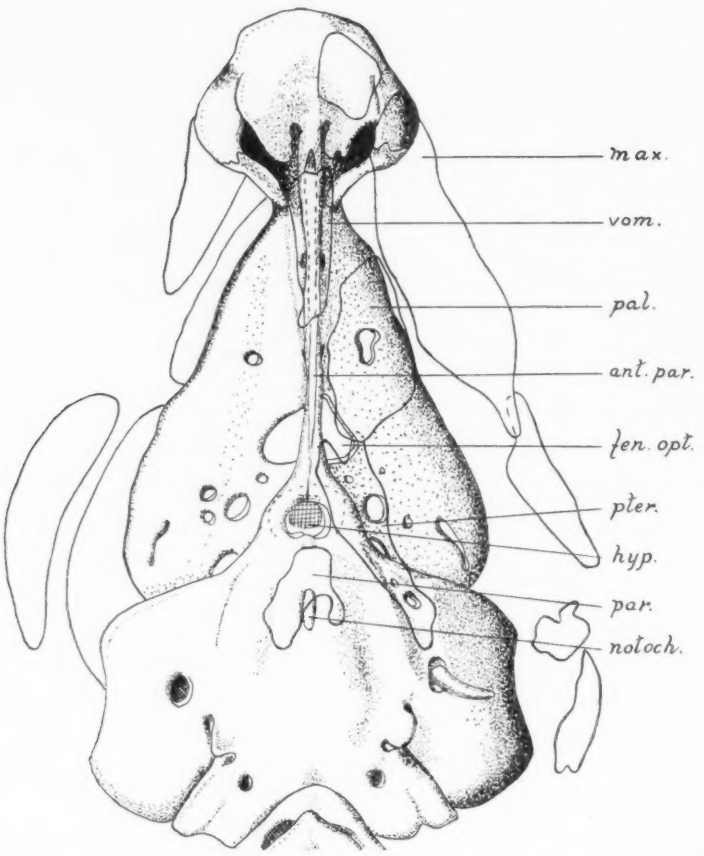

Fig. 1. *Dermochelys coriacea*, 29 days. Ventral view of skull. Outlines of dermal bones indicated. Reconstruction.

extends as a long, narrow, and pointed tongue, in front of the fenestra, sufficiently to reach the level of the fenestra optica.

There is no trace of the parasphenoid to be found in the portion behind the fenestra, at the two younger stages of Dermochelys (19 and 21 days old), obviously because the skull, especially in this portion, is very undeveloped. The state of development of the skull of a 19 days old specimen may be understood from the following brief description (fig. 2). The nasal septum and its continuation caudad, the interorbital septum, consist of blastematic tissue, and of the planum septale there are only irregular streaks of blastema rising from the interorbital septum to the right and left. Behind the primordium of the planum septale is a wide opening, the fissura metoptica, forming a gap at the bottom of which are the trabecles. The trabecles are almost the only parts of the skull where cartilage has formed. Between them is a large

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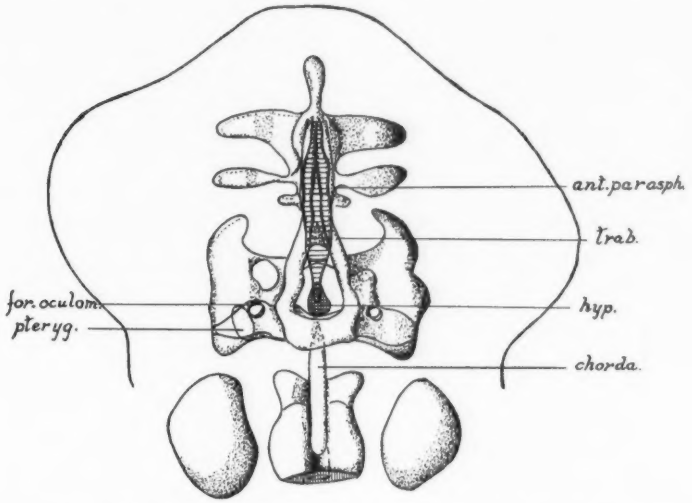

Fig. 2. *Dermochelys coriacea*, 19 days. Ventral view of skull. Reconstruction.

fenestra cranialis anterior. The trabecles join caudally the partly cartilaginous primordium of the basal plate, from which rise the pilae metopticae. This orbital portion of the skull is joined to the parachordal plate solely by means of the notochord. On both sides of the anterior end of the parachordal plate there are situated entirely blastematic otic capsules, still unconnected with the rest of the skull.

In the superficial strata of the sparsely nucleated mesenchyma, that forms the greater part of the head, there are already at this stage, in several places, denser concentrations of nuclei, forming the preblastemas of ultimately developing dermal ossifications. One such place is situated dorso-laterally to the fenestra oculomotoria (fig. 2, pteryg.) where in the 29 days old specimen the posterior end of the pterygoids are formed. Thus this concentration of nuclei represents the pterygoid, in what might be called a preblastematic state.

Another similar concentration of nuclei is found in the shape of a longitudinal band underneath the middle portion of the septum interorbitale. It tapers at both ends, but is plainly visible, contrasting with the surrounding mesenchyma. The posterior end reaches caudad, about as far as to the level of the anterior margin of the fenestra oculomotoria. Thus it protrudes rather far caudad between the trabecles, underneath the fenestra basicranialis anterior. Judging from its shape and position, this stripe of tissue cannot be considered as anything but an anterior portion of the parasphenoid, still at the preblastematic stage (fig. 2).

The changes of the skull at the 21 days old stage include that the planum septale is better developed, though still largely as a blastema, only a small

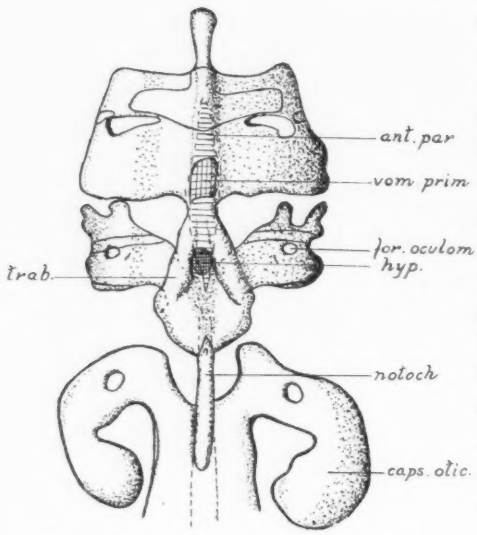

Fig. 3. *Dermochelys coriacea*, 21 days. Ventral view of skull. Reconstruction.

anterior portion being developed as precartilage. It has the shape of two winglike flaps rising from the interorbital septum. The fissura metoptica is still open, but cartilage has developed in the pilae metopticae. Cartilage has also formed between the anterior portions of the trabecles, with the result that the anterior portion of the fenestra basiscranialis anterior has closed. The remaining foramen, the fenestra, or fossa hypophyseos, is about the same size as in the 29 days old specimen. As the fissura metotica is open the skull is still divided in an anterior orbital portion, and a posterior parachordal, and otic, as the otic capsules have now fused with the parachordal plate.

At this stage the anterior parasphenoid primordium is still more plainly differentiated from the surrounding mesenchyma, and might be said to form a real blastema (fig. 3). It has the same shape as before and the posterior end almost covers the fenestra hypophyseos. That is also the case in NICK's ripe embryos, but the difference is that in the older embryos the fenestra is covered from the rear by the rostrum of the ossified posterior parasphenoid, whereas in this young embryo it is covered from the front by the posterior end of the blastema of the anterior parasphenoid. No primordium of the permanent posterior parasphenoid is still visible.

The blastema of the future vomer has also formed (fig. 3) at this stage. It is comparatively short and lies with its posterior rim on the level of the caudal rim of the wing-like orbital cartilage. It is important, for the sake of homologisation of the parasphenoid blastema, that the vomer primordium lies immediately ventrally to it.

In the 29 days old specimen of Dermochelys, where the primordial skull is formed, and chondrified, the blastemas of dermal bones, which had developed at the earlier stages, have also assumed their definite structure and shape. While this applies also to the vomer primordium, the rudiment of the anterior parasphenoid has changed in a regressive direction, whereas the posterior parasphenoid has developed (pag. 3). The reduction of the parasphenoid rudiment shows in the thinning out of the blastema, due to less marked concentration of nuclei. On the other hand the abundant occurrence of collagenous fibers

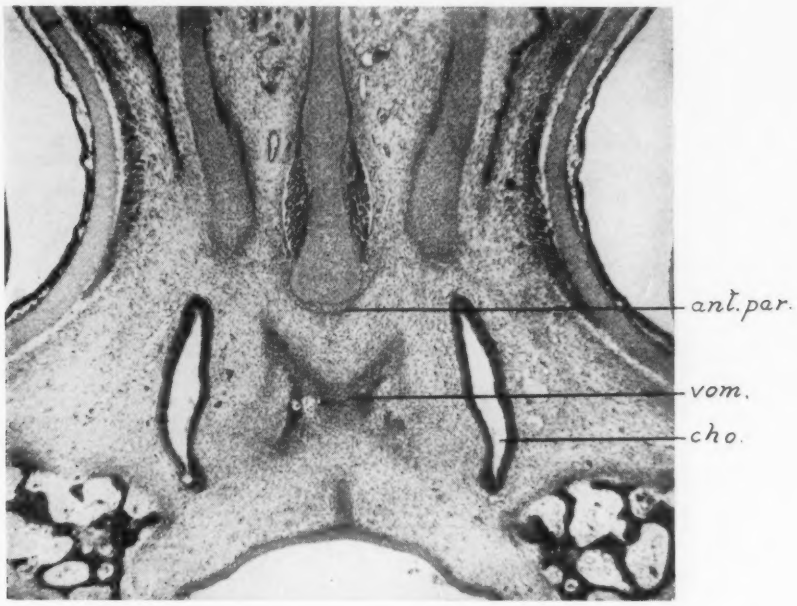

Fig. 4. *Dermochelys coriacea,* 29 days. Cross section through anterior orbital region showing nasal septum, vomer and anterior parasphenoid rudiment.

makes the rudiment still stand out comparatively clearly against the surrounding mesenchyma (fig. 4).

The conditions described now are also encountered in Lepidochelys. The 16 days old specimen of this Cheloniid is considerable further developed than the 21 days stage of Dermochelys (fig. 5). Thus the dorso-lateral edges of the fissura metoptica have closed, and the result is that a fenestra optica, although still very large, has formed. The nasal capsule has begun to develop, the otical portion is comparatively well developed, but a fenestra basicranialis posterior still exists, divided in two halves by the notochord. Only one dermal bone has ossified, the maxillary, in the shape of a slightly curved narrow splint of bone, and in the vomer primordium ossification just has begun. The vomer primordium is very short, and situated ventrally to the anterior parasphenoid rudiment, half way between the anterior and the posterior margins of the orbital cartilage.

As in Dermochelys, blastematic primordia of other dermal bones are developed. Fig. 5 shows the blastema of the future pterygoid rather better developed than in the 21 days specimen of Dermochelys, and in front of it the large primordium of the palatine (fig. 6). The anterior end of the anterior parasphenoid blastema begins on a level with the anterior end of the orbital cartilage. Unlike the parasphenoid blastema in Dermochelys, which was pointed

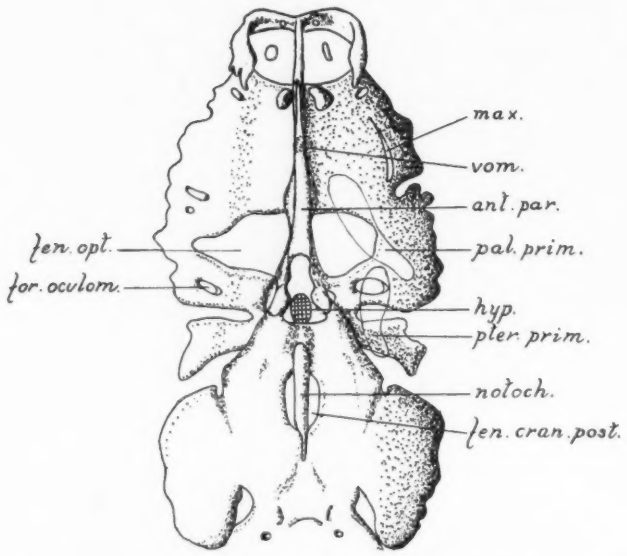

Fig. 5. *Lepidochelys olivacea,* 16 days. Ventral view of skull. Reconstruction.

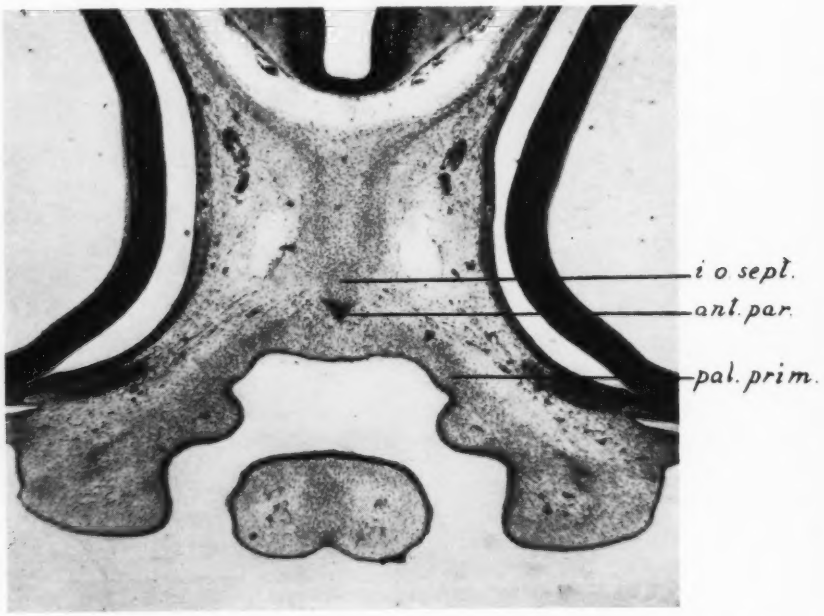

Fig. 6. *Lepidochelys olivacea,* 16 days. Cross section through orbital region anteriorly to the anterior end of the trabecles and showing blastemas of anterior parasphenoid rudiment and of palatine primordium.

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at the both ends, this rudiment spreads out posteriorly, and thus assumes a longitudinal triangular shape. The back edge of this comparatively broad posterior portion has a deep, rounded incision, and covers more than the anterior half of the still rather large fenestra basicranialis anterior. The postero-lateral tips of the primordium extend on each side of the fenestra almost to the level of the posterior rim. What is left uncovered corresponds in size with the future fenestra hypophyseos. No trace of any posterior portion of the parasphenoid is to be seen at this stage.

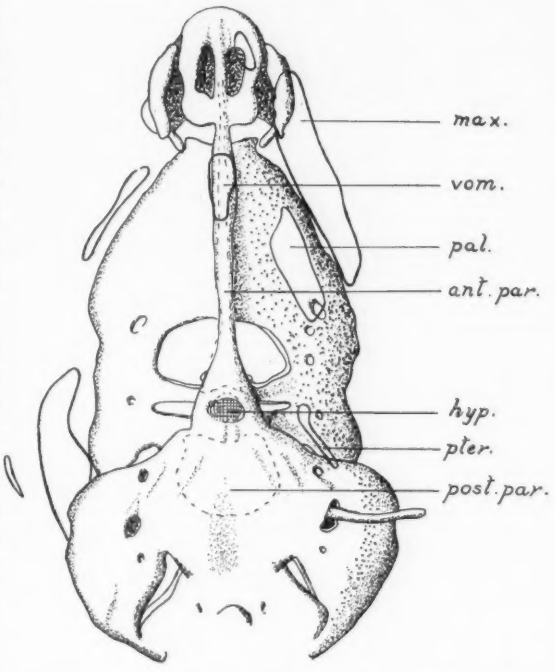

Fig. 7. *Lepidochelys olivacea*, 22 days. Ventral view of skull. Reconstruction.

A 22 days old specimen of Lepidochelys is less developed than the 29 days old Dermochelys specimen, judging from the unfinished nasal capsule, the large fenestra optica, the lack of several dermal bones, and the small size of the ones already ossified (fig. 7). The fenestra basicranialis posterior has closed, and the notochord is entirely embedded in the cartilage of the basal plate.

The anterior parasphenoid rudiment (fig. 7) has about the same shape as at the 16 days old stage, only the indentation at the posterior end is less pronounced. Proportionately, as well as absolutely, it has increased in length, but posteriorly it ends now in front of the fenestra hypophyseos, due to the shortening of this opening in the same way as in Dermochelys.

Another blastema has formed, however, behind the fenestra, exactly in the same place as the ossified parasphenoid is situated in the 29 days old Dermochelys (fig. 7 and 8). It surpasses that bone in size, but does not show any indentation in the posterior rim, where it is evenly rounded. Instead there is a slight curve orad, towards the hypophyseal fenestra.

There is, however, a marked difference in the structure of the two blastemas. The anterior parasphenoid blastema is characterized by a far denser concentration of nuclei than the posterior, where the whole formation is thinner, and less defined. The oldest stage of Lepidochelys I have had the opportunity of examining is a 28 days old specimen. At these later stages the anterior

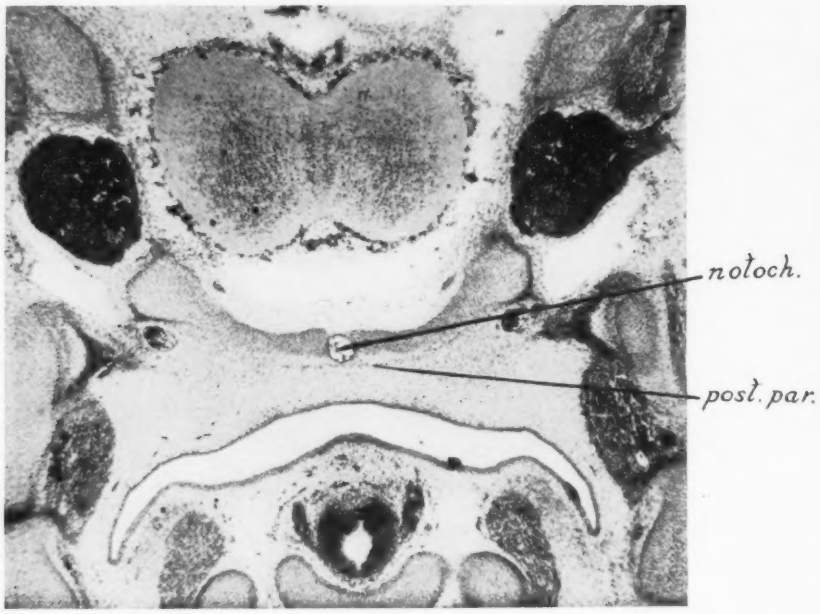

Fig. 8. *Lepidochelys olivacea*, 22 days. Cross section through antotical region showing basal plate, notochord and posterior parasphenoid rudiment.

blastema remains practically in the state described above, whereas the posterior parasphenoid becomes more and more diffuse, and in the end more resembles the stage of the anterior blastema in the 29 days old Dermochelys specimen. Yet, we know that the anterior rudiment represents only a passing embryonic formation, which is to disappear. Whether or not there is really a posterior parasphenoid formed in the Cheloniids is uncertain (cf p. 3). This investigation does not seem to give a definite answer. If anything it tends to give an answer in the negative.

I have also had the opportunity of examining some stages of Chrysemys marginata. Judging from the general development of the primordial skull and the dermal bones, they correspond in relative age to the Lepidochelys specimens described above.

At the youngest stages (head length 4.3—5.0 mm) there is an anterior parasphenoid blastema developed, in shape and size corresponding to the conditions in Lepidochelys, although, perhaps, a little less pronounced. In the oldest of these specimens the regression of the rudiment seems to begin. At the young stages nothing is to be seen of a posterior parasphenoid blastema. An older stage (carapace length 11 mm) seems to correspond in development to the 29 days old Dermochelys, judging from the fact that practically all the dermal bones are well developed, although no beginning perichondrial ossi-

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fication is to be seen. The anterior parasphenoid blastema begins to dissolve, especially the posterior portions. Instead the posterior parasphenoid has appeared as a well developed blastema, where ossification has just begun to take place. The primordium is still comparatively small, and covers the hypophyseal fenestra almost exactly. It is heart-shaped, with the point directed caudad, and situated immediately in front of the notochord, which extends forward as to the posterior margin of the fenestra. In a slightly older specimen (carapace length 12 mm) the posterior parasphenoid is almost entirely ossified. In front it has same shape and extension, but further back it is considerably broader, and extends further back than the posterior margin of the fenestra. Its posterior end continues without any noticeable delimitation in the perichondrial lamella of the basisphenoid which is barely beginning to ossify.

According to earlier investigations on Chelonians, a parasphenoid is reported from Emys (FUCHS, KUNKEL), Chrysemys (SHANER), Chelydra (NICK), Podocnemis (GAUPP) and Dermochelys (VERSLUYS, NICK), thus, from representatives of the Cryptodira, the Pleurodira, and the Athecae. As to the Trionychidae, OGUSHI's paper (1911) on Trionyx japonicus does not give any information, but, from his figures it does not seem improbable, that at least the antero-ventral, portion of the bone, called by him the basisphenoid, might include a parasphenoid element. As to the Cheloniidae, the opinion seems to be unanimous that a parasphenoid is missing (FUCHS, NICK), with NICK's reservation, however that the bone might be discovered at a suitable stage.

The present investigation of Lepidochelys, and Dermochelys, shows, however, not only that a parasphenoid blastema exists even in Cheloniidae, in the place where the bone is formed later in other Chelonians, but that there is also a portion of the parasphenoid found as a blastema, anterior to the fenestra basicranialis anterior.

It is not remarkable in itself that the parasphenoid is formed as two independent portions, an anterior and a posterior, separated by the fenestra basicranialis. The parasphenoid is formed in that way in Amia (PEHRSON, 1940). The anterior portion is formed and ossified before there is anything to be seen of the portion posterior to the fenestra basicranialis. Even if a closer comparison cannot be drawn between Amia and Chelonians, it is obvious that the anterior and first formed portion of the parasphenoid in both is homologous. This anterior portion is further homologous to the crus longitudinale, in Saurians and Rhynchocephalians, to wich it exactly corresponds in origin, shape, and position. In Lacerta (GAUPP) the parasphenoid develops as a pair of primordia, one on each side of the fenestra basicranialis posterior. The rostral portion covers the hypophyseal fenestra from beneath and extends very far orad as the crus longitudinale forms later. According to GAUPP it is uncertain if it forms separately. This is probably the case in skinks according

to SIEBENROCK (1892), where the anterior portion even remains independent. In Lacerta the postero-lateral portions of the parasphenoid fuse with the basisphenoid. DE BEER (1937) states that the parasphenoid in Lacerta develops from one medial (rostral) primordium, under the trabecle comissure, and from paired centres underneath and behind the basitrabecular processes. His statement does not disagree with GAUPP's. Also in Amia the primordium of the posterior portion of the parasphenoid is paired (PEHRSON, 1940).

In Chelonians this posterior portion does not develop as a paired primordium, but on the other hand the bone in Dermochelys when forming shows a deep posterior indentation. Similar conditions are also met with in Emys (KUNKEL) where in an embryo measuring 13.5 mm (carapace length) there is a deep posterior incision. In Chrysemys there is a deep anterior incision. Even in Lepidochelys, where it is doubtful whether a parasphenoid even develops in the adult, there is a faint indication of an anterior incision in the blastema. These conditions might, be interpreted as suggestions of an earlier double origin.

The existence of an anterior parasphenoid blastema in Chelonians should thus be considered to be in accordance with conditions obviously common for many lower vertebrates. This is also the case with the indications of a double origin of the postfenestral portion. In Thalassochelys, as far as is known, the parasphenoid is very well developed in oral direction. Probably it corresponds to both the pre- and the postfenestral portions of the parasphenoid primordium in recent Chelonians. In those the prefenestral portion (a portion which even in Amia has already a certain independence, at least as far as the ontogeny shows) has suffered a reduction, and it exists only as a blastema during a period of the ontogeny.

Even the postfenestral portion is losing its importance in recent Chelonians. In many it fuses, more or less, already during the ontogeny with the basisphenoid, and in Cheloniids it is most probable that it never ossifies as an independent bone. Instead its protective task is taken over by basisphenoid, as is the case in adult specimens of Cheloniids.

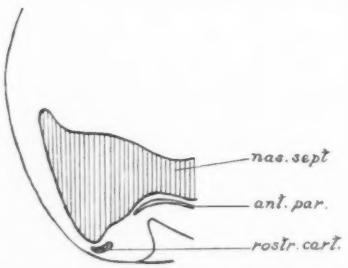

Fig. 9. *Dermochelys coriacea*, 21 days. Sagittal median section through anterior end of the head showing nasal septum, rostral cartilage primordium and anterior parasphenoid rudiment. Reconstruction.

During my investigation of the parasphenoid problem in Dermochelys I was aware of another, only faintly indicated blastema, in the tip of the nose, situated in the mid line ventrally at the anterior end of the interorbital septum. It is comparatively short, cylindrical in shape and lies parallel to the septum.

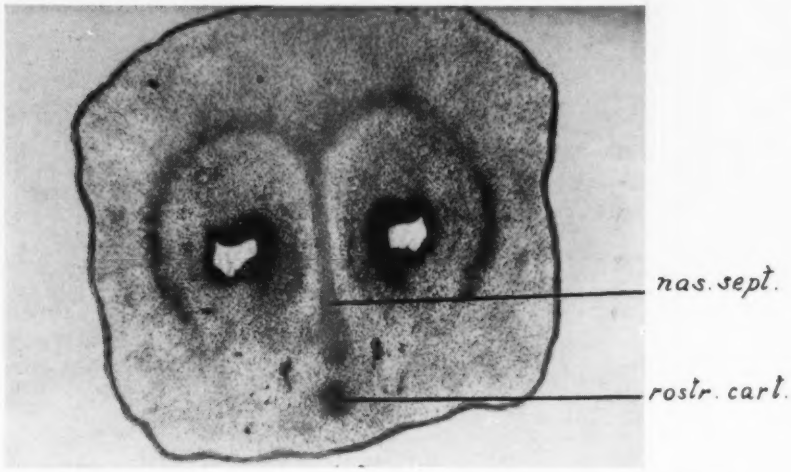

Fig. 10. *Lepidochelys olivacea,* 17 days. Cross section through anterior end of nasal capsule showing rostral primordium.

At the 21 days old stage of Dermochelys (fig. 9) the anterior end seems to be in close contact with the anteroventral tip of the septum. In a 19 days old specimen it has about the same shape and position, but is more difficult to discern, because the anterior end of the septum as well is still at an early blastematic stage. In the 29 days specimen it cannot be traced. In Lepidochelys it turned out to be better developed than in Dermochelys, especially at the 16 and 17 days old stages, where it reaches its highest point of development (figs. 10 and 11). Still, it is plainly visible at the 22 days old stage, although reduction has obviously set in. In Lepidochelys it is quite obviously connected

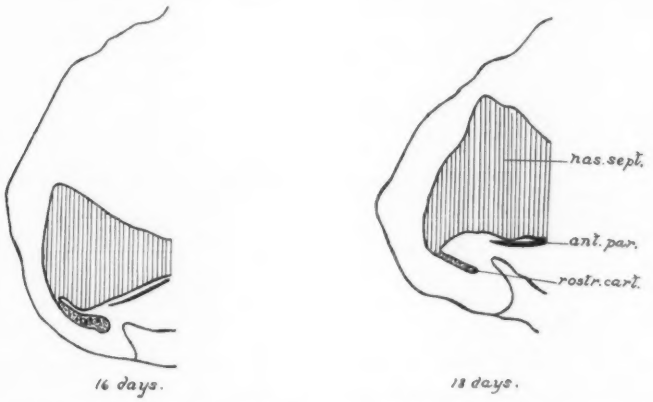

Fig. 11. *Lepidochelys olivacea.* Sagittal median section through anterior end of the head in 16 days and 18 days specimens showing nasal septum, rostral cartilage rudiment and anterior parasphenoid rudiment. Reconstruction.

with the antero-ventral tip of the septum. Posteriorly it reaches so far back that its caudal end, in the 16 days old specimen, is situated slightly behind the anterior end of the parasphenoid blastema, although ventrally to it, as the parasphenoid blastema lies close to the ventral side of the septum.

In the 17 days old specimen of Lepidochelys (fig. 10) the formation consists of fairly well developed prochondrial tissue, almost approaching the structure of real cartilage. Here is therefore the question of a portion of the primordial skull, which forms simultaneously with the ontogenetically older parts of the skull, develops almost to the cartilage stage, and disappears without leaving any traces in the adult. The blastema in Chrysemys is very faintly developed.

After having tried all possible theories applicable on a medial, ventral formation, developing so far orad, my opinion is that it cannot be considered as anything but a rostral process of the skull, but, bent postero-ventrally, possibly in connection with the development of the hook-like bent nose of the Chelonians. The ventral side of the existing tip of the nose of Chelonians should thus be considered as the anterior part of the dorsal side, and the original anterior point of the head of a turtle be situated where, in adult specimens, (and old embryos, — see figs. 9 and 11) the pocket-like anterior portion of the mouth begins.

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THE INTERTRABECLE.

This component of the primordial skull has played a certain part in the morphological discussion, since its first appearance in the literature in 1880, but no definite attempt has been made to investigate the intertrabecle problem thoroughly.

The intertrabecle was first described by PARKER (1880) in his paper on the development of the green turtle, where the fenestra basicranialis in a young embryo (PARKER's 4th stage) is said to be "taken up by three cartilages, the trabeculae and the intertrabecula".

PARKER judged from what he discovered at his 5th stage (about 16 mm carapace length) that "the whole intertrabecular bar is manifestly as much a direct continuation of the mesoblastic sheath of the notochord, as the prochordal parts of the trabeculae are outgrowths of the parachordal tracts". It is evident, from PARKER's description, as well as from his pictures, that what he called the intertrabecula is not only the sagittal cartilage bar in the fenestra basicranialis anterior, but also the continuation forward, the interorbital septum and the nasal septum as far orad as well up in the nasal portion between the walls of the capsule. His figures show, furthermore, that at the fourth stage the intertrabecula does not reach the posterior margin of the

fenestra hypophyseos, and it seems even doubtful if that is the case in the fifth stage, where ossification of the basisphenoid has already started.

PARKER states further that the chondrification at his fourth stage corresponds "very exactly to my first stage in the Selachians. But there the middle part is still soft, and it has not become definite along the middle in the interocular region." The part "along the middle in the interocular region" is where the interorbital septum forms. He says, further, that "in all the Urodeles the intertrabecular cartilage is but feebly developed, and that merely as a conjugation of the trabeculare in the nasal region". It is quite obvious that what PARKER refers to as the intertrabecula is chiefly the cartilage between the anterior parts of the trabecles, whether it does or does not continue caudad to cross the fenestra basicranialis anterior. If there is any ground for interpreting this portion of the septum interorbitale as an independent structure is a question that will be dealt with later on in this paper.

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In accordance with his notion he described the intertrabecle in Crocodile embryos (1881) as the posterior portion of the septum, although it does not protude very far in the hypophyseal fenestra, nor appears as an independent bar between the free posterior portions of the trabecles.

In connection with this it might be mentioned that NICK (1912) seems inclined to consider it not improbable at least that in adult Crocodiles the conditions may resemble those in Chelonia, as the foramen hypophyseos is closed from behind by the tapering anterior end of the basisphenoid, the rostrum basisphenoidale, with which the ventral posterior edge of the cartilaginous septum eventually becomes connected.

FILATOFF (1906) found the intertrabecle at early embryonic stages in so disparate animals as Pristiurus, Emys, and Columba, and based on his discoveries the opinion that it is an organ common to all vertebrates. His description and illustrations show that what he regarded as the developing intertrabecle is the mesenchymatous tissue joining the anterior parts of the trabecles, and developing into the posterior portion of the interorbital septum. KUNKEL (1912) who has given a thorough description of the development of Emys, does not mention any trace of an intertrabecle, and as there is no free intertrabecular bar described in Pristiurus, or Columba either, it is obvious that FILATOFF has adopted PARKER's view on this structure, only that he considers the portion of cartilage developing between the trabecles as the real intertrabecle, whether there is a posterior continuation crossing the foramen hypophyseos or not.

FUCHS (1910) has described the partial occlusion of the fenestra basicranialis anterior, in Cheloniids. According to him the fenestra is first divided by a cartilaginous cross bar in an anterior portion under the hypophysis and a posterior one. This last foramen is then divided by a sagittal bar of cartilage in two foramina for the carotids. He considers this cartilage to be the real

intertrabecle, but in order to avoid confusion with PARKER's intertrabecle in Chelonia, of which this one only corresponds to the posterior end, he prefers to call it the taenia intertrabecularis.

According to FUCHS's description the anterior foramen will later be closed entirely by the trabecles. The cartilage plate that will form the anterior occlusion of the fenestra hypophyseos will thus be formed by fusion of the trabecles, and the anterior end of the taenia intertrabecularis. In a later paper (1912) he repeated his statement, only according to his new investigation the primary fenestra basiscranialis will first be divided sagittally by the growth orad of the taenia intertrabecularis, followed by the division of the anterior portion of the fenestra by the earlier mentioned cross bar. It is important, according to FUCHS, that the original large fenestra basicranialis anterior becomes divided in three foramina, and that the taenia intertrabecularis never reaches the interorbital septum. This opinion, he says, is based on an examination of embryos of Chelonia imbricata.

NICK (1912) does not accept the term given by FUCHS to the free sagittal bar, by way of distinction from PARKER's intertrabecle. Instead he retains PARKER's name but applies it only to this free intertrabecular bar. He points out that in Dermochelys, and in Chelonia mydas, the anterior ends of the trabecles (i. e. the ends of the portions of the trabecles which are free in the stage he has studied) do not fuse with each other, but with a third longitudinal cartilaginous bar in the base of the skull, the intertrabecle, which leaves the dorsum between, and a little below the trabecles. Anteriorly all three join and fuse to a trabecula communis, above which the septum rises in the anterior portion of the orbital region.

The hypophysis, in Chelonia and in Dermochelys, rests on this trabecula communis, chiefly in front of the joining point of the three bars, behind the real orbital septum and not in the fossa hypophyseos where the carotids enter.

NICK has been unable to find any discontinuation between the interorbital septum and the intertrabecle in Chelonia, as mentioned by FUCHS. He considers FUCH's explanation of the formation of the cartilage under the hypophysis in front of the fossa hypophyseos incorrect, and suggests the simpler explanation that the trabecles fuse with the ventral edge of the septum, which grows caudad, closing the anterior portion of the originally comparatively large fenestra basicranialis.

In a ripe embryo of Chelonia mydas NICK found that the intertrabecle had the same thickness as the trabecles. In one of the two ripe embryos of Dermochelys at NICK's disposal the conditions were the same as in the Chelonia embryo. He describes an interesting discrepancy in his other embryo. At the dorsum sellae, and between the posterior ends of the trabecles, is only a short cartilage process, situated above the rostrum parasphenoidale. It is

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strongly curved dorsad. In front of this process the fossa hypophyseos is divided in a right and a left half by a string of connective tissue only, instead of by the intertrabecle. In the anterior portion of the fenestra the intertrabecle appears as a short, pointed, cartilaginous process, between the trabecles, and with its base fused with them. In other words: the intertrabecle is discontinuous, and consists of an anterior, and a posterior portion, both joined by connective tissue. NICK considers this condition as a discrepancy and leaves it at that.

In his opinion the intertrabecle is the caudad prolonged lower edge of the interorbital septum fused with the dorsum sellae. He states further that it still exists in ripe embryos, but dissolves early in the middle, and later disappears almost entirely in Dermochelys, judging from the conditions he has found in adult skulls.

According to VERSLUYS (1936) there is an intertrabecle in Chelone, Dermochelys, Crocodilia and Coluber. It appears either as an independent cartilage bar at the ventral posterior edge of the septum interorbitale, or develops as a process from the crista sellaris growing orad into the fenestra hypophyseos. VERSLUYS supposes there might be the question of quite disparate structures, a possibility also suggested by FUCHS.

Finally DE BEER (1937), who prefers the term taenia intertrabecularis, is of the opinion that the structure in question is proved to exist in the same species as mentioned by VERSLUYS, only he exchanges Coluber for Passer. He interprets NICK's statement concerning the discontinuance of the intertrabecle in one of his ripe Dermochelys embryos as a sign of reduction of the cartilage bar.

From the account given above, concerning earlier investigations of the intertrabecle question, it is evident not only that the views on what should be called the intertrabecle diverge vastly, but also that the ontogeny of this structure is very little known, whether it is considered as chiefly consisting of what seems to be the ventral part of the interorbital septum, or as a structure in itself crossing sagittally the fenestra hypophyseos.

It might be premised at first that BÄCKSTRÖM (1931), in his careful description of the ontogeny of the skull of the grass snake, has not found anything that could be interpreted as an intertrabecle in any sense suggested earlier. A subsequent scrutiny of his numerous series of stages has not revealed anything new. As to Passer, mentioned by DE BEER, there has been no opportunity to obtain material for an investigation.

It seems desirable for the solution of the intertrabecle problem to get an answer to two questions. The first one is: does the cartilage between the anterior parts of the trabecles, where later the ventral edge of the interorbital septum forms, develop ontogenetically in such a way as to be interpreted as a

structure eo ipso as is the opinion first pronounced by PARKER and FILATOFF? The second question is: how does the free intertrabecular bar (taenia intertrabecularis) in Chelone and Dermochelys arise?

The second question will be dealt with first. Investigation on the Dermochelys embryos shows that there is no indication of any taenia intertrabecularis in the youngest stages (figs. 2 and 3). It should be remembered in this connection that at the 19 days old stage the skull still consists chiefly of mesenchyma, cartilage having been formed only in some places, as for instance the trabecles. At this stage the definite fenestra hypophyseos has not yet formed. At the 21 days old stage the chondrification of the skull has included the whole portion between the fissura metoptica and the fissura antotica, and the fenestra basicranialis anterior has shrunk into the fenestra hypophyseos.

In the 29 days old specimen the first indication of a taenia intertrabecularis begins to form in shape of a very short, blunt protuberance from the posterior edge of the fenestra, causing a shallow incisura carotica on each side (fig. 1). The importance of this little process for the origin of the teania will be understood from the conditions encountered in the Lepidochelys specimens. As all the dermal bones of the skull are already developed in the 29 days old specimen of Dermochelys, including the parasphenoid, which always in Chelonians forms later than the other dermal bones, it is clear that at least in this species the taenia intertrabecularis develops very late during the ontogeny.

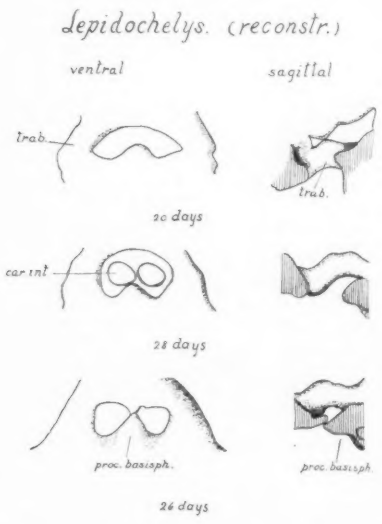

Fig. 12. *Lepidochelys olivacea.* Ventral view and sagittal median section of fenestra hypophyseos in 20, 28 and 26 days specimens. Reconstruction.

An examination of the Lepidochelys stages gave the following result. At the stages younger than 20 days old the conditions were the same as in the youngest Dermochelys specimens, as far as the shape of the fenestra basicranialis anterior is concerned. At the 20 days old stage, however, the fenestra offered about the same view as at the 29 days old Dermochelys stage, thus, a low anteriorly directed protuberance from the middle of the posterior side of the fenestra hypophyseos had developed, causing a shallow incisura carotica (fig. 12). At the nearest following stages the same condition was to be seen, but in the oldest stages, 26 and 28 days old respectively, important changes had taken place. As is often the case the age, respectively the size, of embryonic specimens does not always indicate exactly

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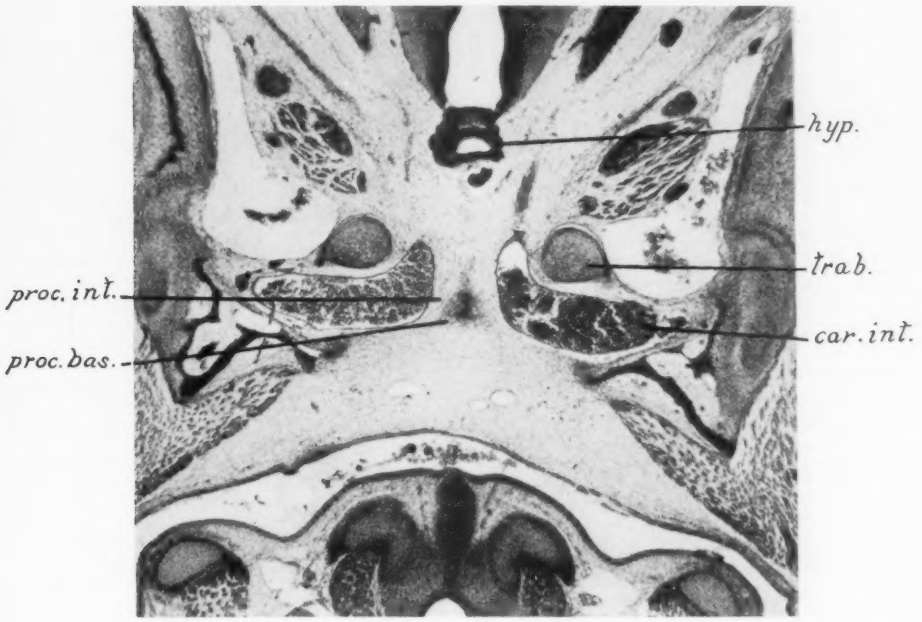

Fig. 13. *Lepidochelys olivacea*, 26 days. Cross section through the fenestra hypophyseos showing posterior portion of the hypophysis, trabecles and ven. carot. int. Between them the tips of processus intertrabecularis (dorsal) and proc. basisphenoidalis. Cf. fig. 12.

the degree of development of special organs, and this is the case in these two specimens of Lepidochelys. The 26 days old specimen, although less developed than the 28 days specimen in several respects, in the size of the dermal ossifications for instance, proved to be more advanced in the development of the taenia intertrabecularis.

In the less advanced 28 days old specimen there is, as in the 20 days old specimen, a posterior process protruding into the fenestra hypophyseos, only at this stage considerably better developed, and causing a quite marked incisura carotica on each side (fig. 12). The question is, thus, whether the taenia intertrabecularis develops as a process from the posterior edge of the fenestra. The answer is given by the examination of the 26 days old specimen. There the posterior process is still better developed, and ending with a pointed tip, but now a similar, only shorter process has formed from the anterior wall of the fenestra (figs. 12 and 13). The anterior process which might be called the processus intertrabecularis is directed slightly dorsad. The tip is overlapping the tip of the straight horizontally directed posterior process. Perichondrial ossification is just beginning in the posterior process, as is seen even where their tips meet. This posterior process is nothing but the rostrum of the future basisphenoid, and should thus be called processus basisphenoidalis.

Probably, although it cannot be proved from my material, as no older stage is available, the processus basisphenoidalis will ossify with at least the tip of the processus intertrabecularis as a continous intertrabecular bar in Lepidochelys and the other Cheloniids. It will therefore divide the fenestra hypophyseos in a right and a left half, as is described from adult specimens of Chelonia.

Thus the "intertrabecle" in NICK's and VERSLUYS's sense consists, chiefly of the rostrum basisphenoidale. It forms very late during the ontogeny, as a matter of fact only just before the beginning of the ossification of the basisphenoid. It is met in front by the intertrabecular process with which it fuses. According to NICK the entire "intertrabecle" in the adult Chelonia is ossified, and forms a long rostrum basisphenoidale, which reaches orad the septum interorbitale. This remains cartilaginous even in adult specimens. NICK's supposition that the "intertrabecle" should be considered as a prolongation of the ventral edge of the septum, which would be growing caudad till it reaches the basal plate, — an opinion undoubtedly supported by PARKER's figures — is not maintainable, judging from the evidence given by the ontogeny of the "intertrabecle" in Lepidochelys.

Further, the development of this structure in Lepidochelys explains the discrepancy in NICK's two ripe Dermochelys embryos. The fact that the "intertrabecle" is discontinous in one of these specimens is probably not due to a reduction of this structure, but proves that it develops in the same way as in Lepidochelys. The insignificant basisphenoidal process in the 29 days old Dermochelys examined by me shows that this stage corresponds, as far as the development of the "intertrabecle" is concerned, to my 22 days old specimen of Lepidochelys. In NICK's ripe embryo the two processes have developed, but not yet sufficiently far to meet. If NICK's description is correct this would have been the case in his other specimen. In Dermochelys, however, the formation of a continous "intertrabecle" is only a passing stage, for, as is evident from NICK's description of skulls of adult specimens, only the posterior end of the "intertrabecle" is left as a more or less ossified blunt projection from the edge of the dorsum sellae.

Contrary to the conditions in Chelonia there is no rostrum basisphenoidale developed in Dermochelys. The function of this structure is no doubt filled in this species by the rostrum parasphenoidale (VERSLUYS, 1909). An "intertrabecle" or, better worded, a taenia intertrabecularis, is encountered in Chelonia (including Caretta and Lepidochelys) and Dermochelys solely. The statement concerning Dermochelys is based only on NICK's description of one of his two ripe embryos. In adult specimens of Dermochelys there exists no taenia intertrabecularis, according to the NICK's evidence. At adult stages there is a taenia intertrabecularis known to exist only in Cheloniids, but neither in other Chelonians nor in any other species. In Cheloniids there is

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no parasphenoid developed. As has been shown earlier in this paper a posterior parasphenoid — the only portion existing in recent Chelonians — is formed during the ontogeny of this group of turtles, but is reduced already during the embryogenesis. The lack of a parasphenoid is therefore a secondary condition in Cheloniids, and the development of a taenia intertrabecularis is limited only to these turtles, where it develops as a substitute for the missing parasphenoid.

Further and more detailed investigations will be necessary for a proper understanding of the conditions in Dermochelys, where there is a vestigial taenia intertrabecularis.

The other question requiring an answer, is whether the cartilage between the anterior parts of the trabecles, where later the ventral edge of the septum interorbitale develops, forms ontogenetically in such a way as to be interpreted as an "intertrabecle" in PARKER's sense. As this question involves problems which lie outside the scope of this paper, and concern the morphogenesis of the chondrocranium of the Chelonians in general, I shall restrict the following account to a short rescription of the conditions encountered chiefly in Lepidochelys and Dermochelys.

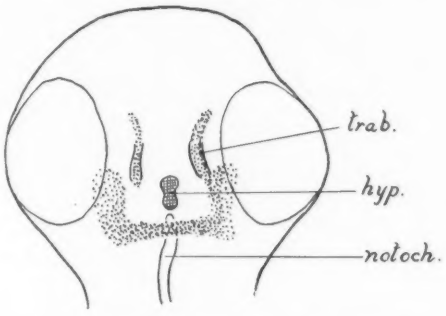

Fig. 14. *Dermochelys coriacea*, 17 days. Dorsal view of skull. Reconstruction.

In a 17 days old specimen of Dermochelys the orbital portion of the skull consists only of the trabecles (fig. 14). They are already partly chondrified and lie as slightly curved rods, comparatively far apart. Their posterior ends are situated on a level with the anterior portion of the hypophysis. A short description of the general features of the skull in a 19 days old specimen is already delivered (page 4). The nasal septum begins to develop at this stage, and the orbital cartilage is seen to form, still only as a mesenchyma. The trabecles have grown considerable in length. Their anterior thirds have approached each other to form a trabecula communis, in which, however, the two components still retain their independence and have not fused. There is a comparatively long fenestra basicranialis anterior (fig. 2) behind their still free posterior portions. The anterior termination of this fenestra is formed by mesenchymatous tissue, developed between the middle portion of the trabecles. Although this tissue is comparatively well outlined against both the cartilage of the trabecles, and the mesoblastic tissue above and below, it can hardly be described as forming a definite string, or body.

At the 21 days old stage the tissue between the trabecles has changed into

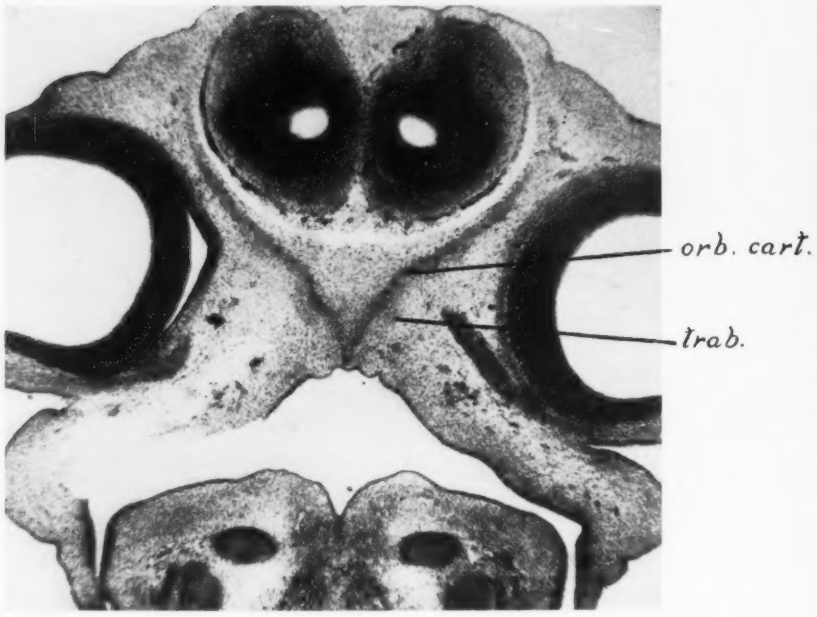

Fig. 15. *Lepidochelys olivacea*, 15 days. Cross section through orbital region showing orbital cartilage and anterior ends of the trabecles.

cartilage, and grown still further caudad. The result is that the fenestra has now diminished considerably in front, and assumed the shape of the fenestra hypophyseos (fig. 3). It is, however, not possible to characterize the tissue between the trabecles as a structure in itself, independent of the trabecles and the developing orbital cartilage. Yet the posterior end of the trabecula communis, formed by the trabecles and the cartilage in between, forms three parallel ridges, indicating the origin from three components, the trabecles and the — literally speaking — intertrabecular cartilage.

In the 29 days old specimen the conditions have altered so radically through the development of the septum interorbitale, that every trace of the trabecles, except the free parts encircling the fenestra hypophyseos, is effaced.

From what is found at these Dermochelys stages an intertrabecle in PARKER's sense in this species can handly be said to exist, as the intertrabecular tissue does not develop from a structure sufficiently sharply defined from the trabecles. This is probably due to the fact that in the stages where three separate ridges should be formed, the anterior ends of the trabecles have formed a sort of trabecula communis, leaving no space between them for any intertrabecular structure.

In Cheloniids — judging from the conditions in Lepidochelys — the situation is different. There the trabecles never approach as closely as in Dermochelys,

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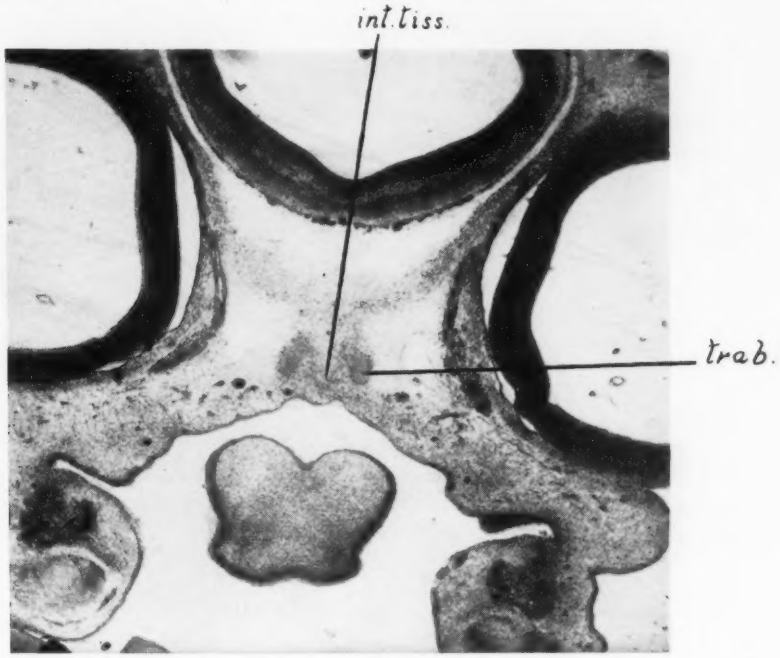

Fig. 16. *Lepidochelys olivacea*, 15 days. Cross section through orbital region further back than in preceding fig. Between the trabecles "intertrabecular" string of tissue.

which means that a trabecula communis is not formed. The anterior portion of the skull consists of prochondrial tissue at the 15 days old stage. Real cartilage has formed only in the place where the mm. recti int. insert. A little caudad from this point the anterior ends of the trabecles are connected laterally with the orbital cartilage, which in the cross section is V-shaped (fig. 15). The trabecles are free still further caudad. Between them is a mesenchymatous string which will later form the septum interorbitale (fig. 16). It is connected anteriorly with the keel-like ventral edge of the orbital cartilage, a portion which will form the anterior part of the interorbital septum. Still further orad this keel-like edge is connected with the primordium of the septum nasi. Purely topographically speaking, the mesenchymatous intertrabecular string is the posterior end of the septum growing caudad.

In a 16 days old specimen of Lepidochelys a distinct through still low septum has developed. It is connected with the trabecles from a point about on a level with the entrance of the optic nerve in the eyes. Further caudad, but still in the interorbital region, the septum, when seen from the ventral side, appears as a distinct ridge between the two ridges formed by the trabecles (fig. 17). This median ridge is the intertrabecle in PARKER's sense. The head length at this stage is 6.5 mm, in PARKER's fourth stage, measured in his

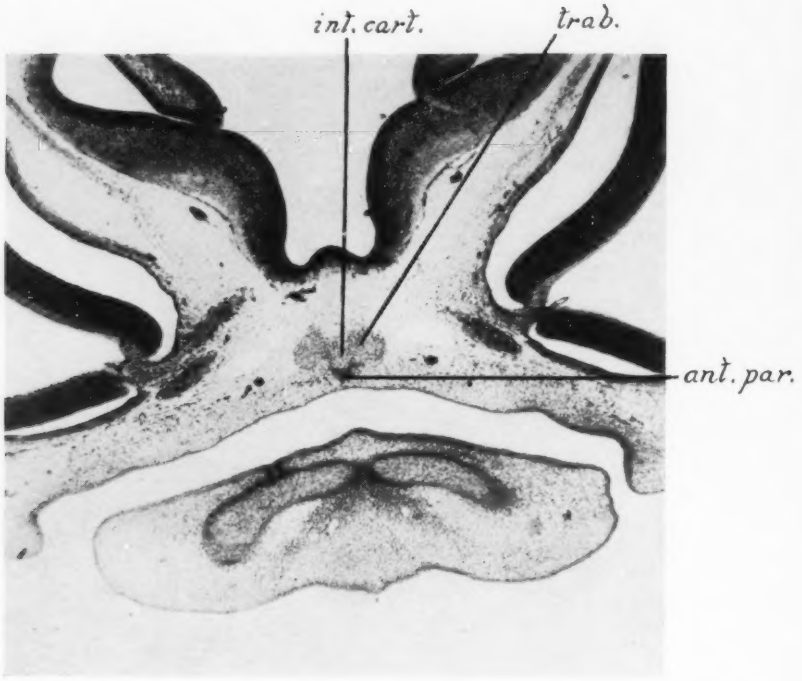

Fig. 17. *Lepidochelys olivacea*, 16 days. Cross section through orbital region showing trabecles and "intertrabecular" cartilage.

illustration it is 4.7 mm. It has already been mentioned (page 18), that there is no taenia intertrabecularis formed in Lepidochelys at this stage.

At the 18 days old stage of Lepidochelys the three ridges are still more distinctly visible on the edge of the septum from the entrance of the optic nerve in the eyes, and caudad to the edge of the hypophyseal region. The head length at this stage is 7.1 mm.

In the next following older stages the septum is still visible as a medial ridge between the trabecles, but as the septum is growing thicker the trabecles get proportionally thinner (fig. 18). In the same time they are pushed relatively further back, as the entire interorbital region is growing in length. At the oldest of these stages, a 21 days old specimen, the septum has already lost its appearance of an intertrabecular bar because of the difference in size between the three components. The head length at this stage is 9.3 mm, in PARKER's fifth stage 8.9 mm.

The same conditions as in Lepidochelys can be observed in Chrysemys. At two stages of Chrysemys marginata (head length 3.5 and 3.6 mm respectively) a distinct median bar of cartilage is formed in the interorbital region between the trabecles. Its oral portion forms the septum nasi and the rest

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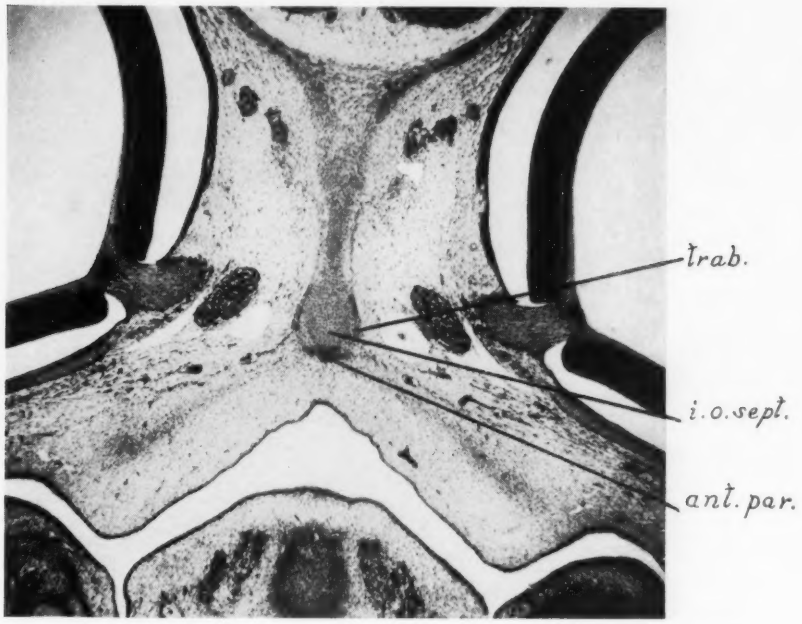

Fig. 18. *Lepidochelys olivacea*, 19 days. Cross section through orbital region showing interorbital septum with anterior ends of trabecles. Below, anterior parasphenoid rudiment.

the low interorbital septum. These two portions pass into each other without any noticeable delimitation. In the interorbital region the trabecles are connected with the median bar, (the interorbital septum) and thus three distinct parallel ridges are seen. In a slightly older specimen (head length 3.9 mm) the posterior end of the median bar is even protruding into the anterior end of the fenestra basicranialis. As in Lepidochelys, however, there is no sign of an intertrabecular process once the anterior portion of the fenestra has closed and the fenestra hypophyseos is formed. In Lepidochelys such a process develops at a still later stage, as already mentioned, and forms the anterior portion of the taenia intertrabecularis, but in Chrysemys no such structure develops. As might be expected no trabecula communis is formed in Chrysemys hence the great resemblance to Lepidochelys.

An intertrabecle, in PARKER's sense, is thus developed not only in Cheloniids, but also in Chrysemys. As the structure in question is the developing interorbital septum it is probable that it might be discovered in other Chelonians as well, and even in other animals where no real trabecula communis forms.

This side of the intertrabecular problem is thus part of another: how does the interorbital septum arise? This problem will not be dealt with in the present paper, as previously mentioned. So much might however be said,

that the formation of a distinct intertrabecular bar, during some period of the ontogeny, is chiefly dependent on the relative position of the trabecles.

As to the Crocodiles, also mentioned by PARKER, I have had the opportunity of examining two young embryonic stages of Crocodilus niloticus, (head length about 5 mm and 12 mm respectively) as well as one of Alligator sp. (head length 17 mm). In the youngest specimen there is no cartilage formed. A very blunt processus basisphenoidalis is to be seen at the posterior rim of the still very long fenestra basicranialis. In the older specimen of Crocodilus, where cartilage has formed and the fenestra is considerably shortened, there is a short processus basisphenoidalis, but no indication of any processus intertrabecularis. Anterior to the fenestra hypophyseos there is a faint indication of three parallel ridges. The skull in the Alligator specimen is much better developed, and dermal bones are already beginning to form. There is hardly any proc. basisphenoidalis to be discerned, and no trace of an intertrabecular process, nor of any ridges in the septum. NICK's supposition that an intertrabecle might develop in Crocodiles could not therefore be proved.

Finally I want to mention that I have not found in any of the Lepidochelys series that the anterior portion of the fenestra basicranialis anterior closes by means of the development of a transversal cartilage bar, as stated by FUCHS (1910 and 1912) to be the case in Chelonia imbricata. Nor has NICK been able to discover any such structure in Chelonia.

SUMMARY.

In the Chelonians examined (Chrysemys, Lepidochelys and Dermochelys) a distinct parasphenoid primordium forms anterior to the hypophysis at a very early stage during the ontogeny, exactly as is the case in Amia. This anterior primordium, which is homologous to the anterior portion of the parasphenoid in lower vertebrates, is only an embryonic structure, and reduces during the late period of the ontogeny. Later, but before the reduction of this anterior parasphenoid portion has started, the blastema of the definite parasphenoid in Chelonians forms behind the fenestra hypophyseos. In Dermochelys and Chrysemys it ossifies, but reduces in Lepidochelys before the end of the ontogeny. The opinion based on examinations of skulls of adult Cheloniids that a parasphenoid is lacking in this group is thus confirmed.

The name intertrabecle is used in two different senses. In PARKER's sense, which has priority, the intertrabecle is a structure forming between the trabecles in their entire length, in Chelonia also protruding into the fenestra hypophyseos from the front. This intertrabecle is, according to the present investigation, the future interorbital septum, discernable as a ridge between the trabecles in Lepidochelys and Chrysemys, where the trabecles remain

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separate in their whole length during the ontogeny. It does not form in Dermochelys where the anterior portions of the trabecles join to form a trabecula communis. In which way the septum interorbitale arises is not discussed in the present paper.

According to the other notion the intertrabecle, or taenia intertrabecularis, is a sagittal bar dividing the fenestra hypophyseos in a right and a left half. This taenia develops in Lepidochelys and Dermochelys comparatively late during the ontogeny from a posterior processus basisphenoidalis and an anterior processus intertrabecularis. In adult turtles it exists only in Cheloniids in the shape of the ossified rostrum basisphenoidale, where it has taken the function of the rostrum parasphenoidale, as a parasphenoid is missing in this group of Chelonians.

An "intertrabecle", in the first sense, may arise wherever the conditions mentioned above are present. The structure in the second sense seems to exist only in Cheloniids amongst lower vertebrates.

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LIST OF ABBREVIATIONS.

ant.par., anterior parasphenoid rudiment.
caps.otic., capsula otica.
car.int., vena carotis interna.
cho., choanas.
fen.opt., fenestra optica.
fen.cran.post., fenestra basicranialis posterior.
for.oculom., foramen nervi oculomotorii.
hyp., hypophysis.
i.o.sept., interorbital septum.
int.cart., "intertrabecular" cartilage.
int.tiss., "intertrabecular" tissue.
max., maxillary.
nas.sept., nasal septum.
notoch., notochord.
orb.cart., orbital cartilage.
pal., palatinum.
pal.prim., palatine primordium.
par., parasphenoid.
post.par., posterior parasphenoid rudiment.
proc.bas., processus basisphenoidalis.
proc.int., processus intertrabecularis.
pter., pterygoid.
pter.prim., pterygoid primordium.
rostr.cart., rostral cartilage.
trab., trabecle.
trab.comm., trabecula communis.
vom., vomer.
vom.prim., vomer primordium.

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